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Maine Agricultural Experiment Sta

ORONO

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MODE OF INHERITANCE OF FECUNDITY IN DOMESTIC FOWL

This bulletin gives a detailed, technical account of the latest results of the experiments in breeding for egg production at this Station. The manner in which the productive ability (fecundity) of hens is inherited is described.

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BULLETIN No. 205.

THE MODE OF INHERITANCE OF FECUNDITY IN THE DOMESTIC FOWL[1]

RAYMOND PEARL

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[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station No. 37. An abstract of this paper was presented at the meeting of the American Society of Naturalists in Princeton, N. J., December, 1911. The present paper was first published in the Journal of Experimental Zoölogy, Vol. 13, No. 2, August 1912, pp. 153-268.

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Introduction

During the course of an investigation into the inheritance of fecundity in the domestic fowl, which has now involved thirteen generations and several thousand individuals, and has occupied the major portion of the writer's time during the past five years, two definite and clear-cut results have come to light.[2] These are:

First: that the record of egg production or fecundity of a hen is not of itself a criterion of any value whatsoever from which to predict the probable egg production of her female progeny. An analysis of the records of production of large numbers of birds shows beyond any possibility of doubt that, in general, there is no correlation between the egg production of individuals and either their ancestors or their progeny.

[2] For a complete list to date of the publications, in which the results of the investigation referred to have appeared, see the bibliography at the end of this paper. Throughout this paper numbers in parentheses refer to titles in the bibliography.

Second: that, notwithstanding the fact just mentioned, fecundity is, in some manner or other, inherited in the domestic fowl. This must clearly be so, to mention but a single reason, because it has been possible to isolate and propagate from a mixed flock 'pedigree lines' or strains of birds which breed true, generation after generation, to definite degrees of fecundity. Some of these lines breed true to a high condition or degree of the character fecundity; others to a low state or degree of this character.

Definite as these results are they give no clue as to how fecundity is inherited; what the mechanism is. Plate (43) has recently said: "Das Ziel der Erblichkeitsforschung muss die Aufstellung von 'Erbformeln' für alle untersuchten Merkmale sein." This expresses the case precisely. To determine the 'Erbformeln' of fowls with respect to fecundity has been the goal towards which every part of the present investigation has been directed and urged. It is believed that a first approximation to the solution of the problem has now been reached. While there remain obscure points still to be cleared up, yet the results now in hand appear to indicate pretty clearly the general character of the mechanism of the inheritance of fecundity, and to show what lines further investigation of the problem may most profitably take. It is the purpose of this paper to present an account of the results mentioned. In doing this it will be necessary to bring forward evidence of several distinct sorts, anatomical and physiological as well as genetic. Only by approaching this problem of the inheritance of fecundity from all angles has it been possible to gain that understanding of the character itself which, in this instance certainly, is absolutely essential to a correct interpretation of any results respecting its inheritance.

BIOLOGICAL ANALYSIS OF THE CHARACTER FECUNDITY

At the outstart it will be well to understand clearly what is meant by the term fecundity as here used. In a former paper (34) the terms 'fecundity' and 'fertility' were defined as follows, and have been used as there defined throughout the course of the investigation:

We would suggest that the term 'fecundity' be used only to designate the innate potential reproductive capacity of the individual organism, as denoted by its ability to form and sepa-

rate from the body mature germ cells. Fecundity in the female will depend upon the production of ova and in the male upon the production of spermatozoa. In mammals it will obviously be very difficult, if not impossible, to get reliable quantitative data regarding pure fecundity. On the other hand we would suggest that the term 'fertility' be used to designate the total actual reproductive capacity of pairs of organisms, male and female, as expressed by their ability when mated together to produce (i. e., bring to birth) individual offspring. Fertility, according to this view, depends upon and includes fecundity, but also a great number of other factors in addition. Clearly it is fertility rather than fecundity which is measured in statistics of birth of mammals.

Taking fecundity as above defined it is obviously a character depending upon the interaction of several factors. In the first place the number of ova separated from the body by a hen must depend, in part at least, upon an anatomical basis, namely, the number of ova present in the ovary and available for discharge. Further there must be involved a series of physiological factors. The mere presence of an anatomically normal reproductive system, including a normal ovary with a full complement of ova, and a normal oviduct, is not enough to insure that a hen shall lay eggs, that is, exhibit actual as well as potential fecundity. While comparatively very rare, cases do occur in which a bird possesses a perfect ovary and perfect oviduct and is in all other respects entirely normal and healthy, yet never lays even a single egg in her life time. Such cases as these prove (*a*) that what we may call the anatomical factor is not alone sufficient to insure that potential fecundity shall become actual, and (*b*) that the anatomical and physiological factors are distinct, in the sense that the normal existence of one in an individual does not necessarily imply the co-existence of the other in the same individual.

A case of this kind is found in hen no. 8051 hatched March 29, 1909, and killed for autopsy record August 24, 1911. This bird had the secondary sexual characters of the female perfectly developed, and was entirely normal in other respects (body weight, 2366 grams). This bird never laid an egg during its life. The ovary was normal (fig. 450) and was of about the size proper to a fully developed pullet just reaching the point of beginning to deposit yolk rapidly in certain oöcytes in preparation for laying. While counts were not made this ovary

appeared to carry a normal number of oöcytes. In general it was anatomically normal, but physiologically in the state of development appropriate to a five or six months old pullet just about to lay. The same was true of the oviduct. In this case the physiological factor or factors necessary to the bringing about of ovulation were simply totally lacking, in an otherwise perfectly normal bird.

Some other cases demonstrating the same thing might be cited from our records, but this will suffice for present purposes.

Turning now to the physiological factors involved in fecundity it would appear that there are at least two such factors or

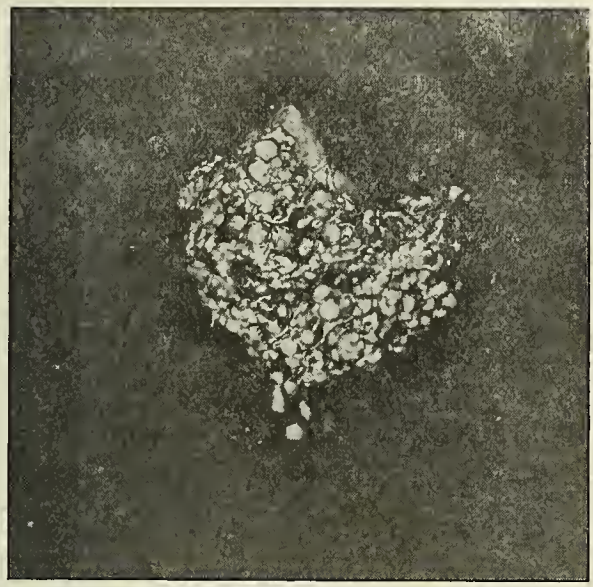

Fig. 450. Photograph (about twice natural size) of ovary of hen No. 8051. Note the presence of a large number of oöcytes; none of which is enlarging in preparation for laying. See text for further explanation.

groups of factors. The first of these may be designated as the 'normal ovulation' factor. By this is meant the complex of physiological conditions which taken together determine the laying of about such a number of eggs as represents the normal reproductive activity of the wild Gallus bankiva. Under conditions of domestication the activity of this normal ovulation factor will mean the production of more eggs than under wild conditions. Continued egg production involves certain definite and rather severe metabolic demands, which under wild condi-

tions will not always, or even often be met. Further, as has been especially emphasized by Herrick (18, 19, and other papers), egg laying in wild birds is simply one phase of a cyclical process. If the cycle is not disturbed in any way the egg production is simply the minimum required for the perpetuation of the race. If, however, the cycle is disturbed, as for example, by the eggs being removed from the nest as fast as they are laid, a very considerable increase in the total number of eggs produced will result. This, of course, is what happens under domestication. What an effect in increasing the actual expressed fecundity of a wild bird the simple removal of eggs as fast as they are laid may have, may be illustrated by three cases from the literature. Austin (1) shows that whereas the wild Mallard duck in a state of nature lays only 12 to 18 eggs in the year, it will lay from 80 to 100 if they are removed as fast as laid and the bird is kept confined in a pen at night. Hanke (16) by regularly removing the eggs got 48 in succession from a common wryneck (Iynx torquilla[3]). Wenzel (53) in the same way brought a house sparrow's productivity up to 51 eggs.

With the domesticated Gallus the 'normal ovulation' factor may be taken as inducing a production of anything up to from forty to eighty eggs in a year, this production being spread over the period of from sometime in February to September or October. In this physiological complex are involved the elaboration and deposition of yolks, the rapid growth of a few oöcytes just preceding ovulation, ovulation itself, the activation of the oviduct, etc. The details of some of the processes involved have been described elsewhere (cf. Rubaschkin (44), Sonnenbrodt (48), Pearl and Curtis (33) and Pearl and Surface (37)) and do not concern us here. The essential point to be noted is that in this normal ovulation factor we are dealing with the basic physiological processes of normal 'unimproved' laying. To make a normal laying hen it is necessary to have present both the anatomical basis discussed above and the physiological basis, which has been designated the normal ovulation factor.

It is a fact well known to poultrymen, and one capable of

[3] I give this scientific name with much hesitation, not knowing what pranks the rule of priority or other nomenclatorial disturbers of the peace may have played with it in recent years. In any event the common name will quite sufficiently indicate what bird it is that is here under discussion.

easy observation and confirmation, that different breeds and strains of poultry differ widely in their laying capacity. In saying this the writer would not be understood to affirm that a definite degree of fecundity is a fixed and unalterable characteristic of any particular breed. The history of breeds shows very clearly that certain breeds now notably poor in laying qualities were once particularly good. One of the best examples of this is the Polish fowl. But, in spite of this, inheritable breed and strain differences in fecundity exist, and probably always have existed. Such inheritable differences are independent of feeding or any other environmental factors. Thus the strain of Cornish Indian Games with which I have worked are poor layers, regardless of how they are fed or handled. This is merely a statement of particular fact; it does not imply that there may not exist other strains of Cornish Indian Games that are good layers.

The difference between this strain of Cornish Indian Games and Barred Plymouth Rocks, when kept under the same conditions and managed in the same way, is shown in tables 1 and 2, which give the frequency distributions and constants respectively, for flocks of these breeds kept at the Maine Station. The birds included in table 1 were all pullets, hatched at approximately the same time, and reared, housed, fed and cared for in all respects similarly. The Plymouth Rock distribution includes birds of both high and low fecundity strains. The low producing birds lower the mean in what is really an unfair manner, so far as concerns breed comparisons. The point is that, in the work of the Station, low-producing lines have been propagated for experimental purposes to a much greater extent than would be the case in purely random breeding of the Maine Station's stock of the Barred Plymouth Rock breed. To make a perfectly just comparison between Cornish Indian Games and Barred Rocks, the strains of the latter deliberately bred for low egg production should be excluded. It has, however, in the present case been deemed best to take the whole flock of Barred Rock pullets for the laying year 1910-11, without any selection. The comparison is sufficiently striking even on this basis.

TABLE 1

Frequency distribution of winter egg production of the Barred Plymouth Rock and Cornish Indian Game breeds

Eggs Laid in Winter Period	Barred Plymouth Rocks Laying the Specified Number of Eggs.		Cornish Indian Games Laying the Specified Number of Eggs.	
	Absolute number	Per cent. of flock	Absolute number	Per cent. of flock
0–5	43	14.4	32	48.5
6–11	22	7.4	8	12.1
12–17	28	9.4	9	13.6
18–23	19	6.3	6	9.1
24–29	25	8.4	7	10.6
30–35	26	8.7	1	1.5
36–41	19	6.4	3	4.5
42–47	27	9.0		
48–53	16	5.4		
54–59	21	7.0		
60–65	14	4.7		
66–71	10	3.3		
72–77	9	3.0		
78–83	3	1.0		
84–89	3	1.0		
90–95	0			
96–101	8	2.6		
102–107	0			
108–113	4	1.3		
114–119	2	0.7		
Total . .	299	100.0	66	99.9

From tables 1 and 2 it will be noted that:

1. The mean winter production of the Cornish Indian Games is less than one-third that of the general flock of Barred Plymouth Rocks, under uniform environmental conditions.

2. The winter production of the Games is considerably less than a fourth of that of the high producing lines of the Barred Rocks.

3. The variabilities in both cases are high, but relatively not significantly different. It is of interest to note that the observed coefficients of variation for winter production here given are of the same order of magnitude as the mean coefficients for the laying of the four winter months, November, December, Janu-

ary and February. Taking the mean of the coefficients of variation for these four months as given by Pearl and Surface (37. table 5, p. 96) we get 95.15.

TABLE 2

Constants for variation in winter egg production of the Barred Plymouth Rock and Cornish Indian Game breeds

Breed	Mean	Standard deviation	Coefficient of Variation
	Eggs	*Eggs*	*Per cent.*
Barred Plymouth Rock	36.35 ± 1.04	26.69 ± 0.74	73.42 ± 2.92
Cornish Indian Game	11.64 ± 0.88	10.61 ± 0.62	91.15 ± 8.73
Differences	+24.71 ± 1.36	+16.08 ± 0.97	—17.73 ± 9.21
Barred Plymouth Rock:			
All High Lines in 1908–09[1]	54.16		
All High Lines in 1909–10[1]	47.57		
All High Lines in 1910–11[1]	50.58		

[1] Figures taken from Pearl (28).

The inferiority in egg production of the Cornish Indian Games is most strikingly shown by the integral curves from table 1. In table 3 the integral curves are given (in inversed form) for the winter production of Barred Rock and Cornish fowls.

The data of table 3 are shown graphically in figure 451.

This diagram is to be read in the following manner. The percentages of the flock laying a specified number of eggs are plotted on the abscissal axis. The different egg productions are plotted as ordinates. From the diagram it appears (for example) that whereas 47 out of every 100 birds in the Barred Rock flock each produced 35 or more eggs in the winter period, only 4 and a fraction birds out of every 100 in the Cornish Indian Game flock were able to produce as many eggs as this—35—in the same period.

Now in individuals which are high layers, and have this characteristic in hereditary form, there must be involved some further physiological factor in addition to the normal ovulation factor already discussed. An analysis of extensive statistics has shown (36, 37) that high fecundity represents essentially an addition of two definite seasonal, laying cycles to the basic, nor-

TABLE 3

Showing the percentage of the whole flock producing in the winter period more than certain specified numbers of eggs, in the case (a) of Barred Plymouth Rocks and (b) of Cornish Indian Games

The Indicated Percentage of the Flock Produces in the Winter Period	Barred Plymouth Rock	Cornish Indian Game
6 or more eggs	85.6	51.5
12 or more eggs	78.2	39.4
18 or more eggs	68.8	25.8
24 or more eggs	62.5	16.7
30 or more eggs	54.1	6.1
36 or more eggs	45.4	4.6
42 or more eggs	39.0	0
48 or more eggs	30.0	0
54 or more eggs	24.6	0
60 or more eggs	17.6	0
66 or more eggs	12.9	0
72 or more eggs	9.6	0
78 or more eggs	6.6	0
84 or more eggs	5.6	0
90 or more eggs	4.6	0
96 or more eggs	2.0	0
102 or more eggs	2.0	0
108 or more eggs	0.7	0
114 or more eggs	0.7	0
120 or more eggs	0	0

mal reproduction cycle. These added periods of productivity are what may be called (cf. 37, 28, 30) the winter cycle and the summer cycle. The winter cycle is the more important of these. It is the best practical measure of relative fecundity which we have and has been used as the chief unit of fecundity in these studies. It constitutes a distinct and definite entity in fecundity curves. The existence of this added fecundity, in high laying birds must depend upon some additional physiological factor or mechanism besides that which suffices for the normal reproductive egg production. Given the basic anatomical and physiological factors the bird only lays a large number of eggs if an additional factor is present.

As to the nature of this physiological mechanism we can only speculate. It probably involves fundamentally such matters as

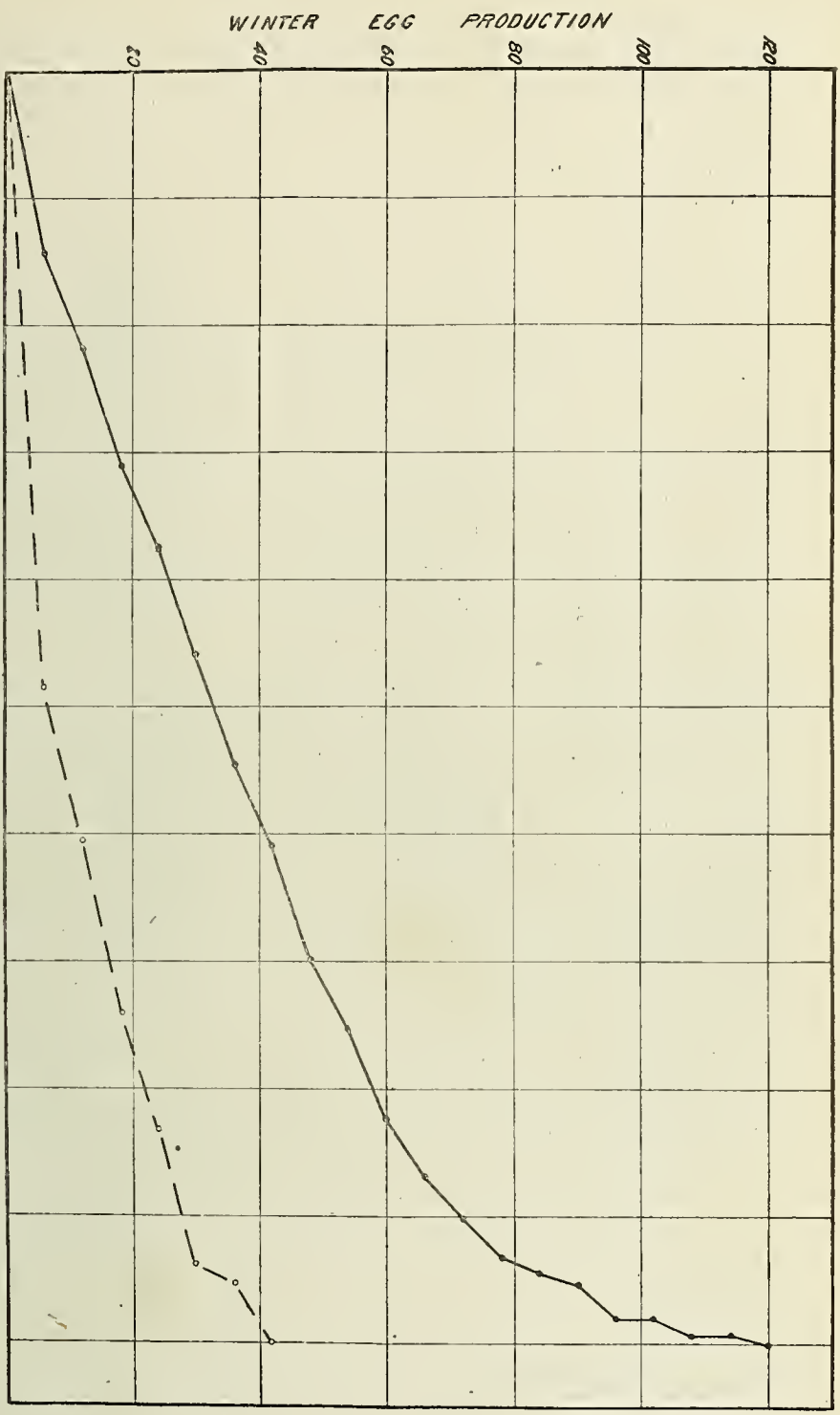

Fig. 451. Integral curves of winter egg pro duction of Barred Plymouth Rock and Cornish Indian Game pullets. Solid line—Barred Plymouth Rocks. Broken line—Cornish Indian Games.

more perfect metabolism, including the distribution of substance and energy to the ovary, on which very heavy demands are laid in a high fecundity record. Immediately it involves a control of the process by which the supply of oöcytes on the ovary in the final stages of rapid growth by yolk deposition is kept at a relatively high level for long periods of time. Sonnenbrodt's (48) work suggests that the interstitial cells of the ovary may be connected with the process. Thus he says (loc. cit., p. 421): "Bei älteren Hühnern findet man die Zwischenzellen immer noch, und besonders in der Nähe der Gefässe. Sie liegen hier gruppen-und nesterweise zwischen den Follikeln und *vor allem auch in den Stielen der grösseren Follikel,*[4] immer dort, wo besonders starke Blutzufuhr günstige Ernährungsbedingungen bietet."

It is quite conceivable that the presence of numerous interstitial cells on the stalks of the follicles of rapidly growing oöcytes is a cause of the rapid growth rather than an effect, as Sonnenbrodt suggests. The whole subject of the intimate physiology of the ovary needs more study.

Whatever the precise nature of the factor under discussion, which is a matter for future investigation, the main points which appear clear at present are that: (*a*) high fecundity represents a definite addition to the normal egg production sufficient in amount for purposes of reproduction. This added fecundity has been shown (cf. 28, 30) to be definitely inherited in certain cases at least and may be regarded as dependent on or determined by some physiological factor or complex of factors not present in birds which exhibit a low degree of fecundity.[5]

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[4] My italics.—R. P.

[5] Throughout this discussion it is presumed that the reader will understand without repeated specific statements that attention was paid to environmental factors in the experimental work. That is, when the statement is made that one bird or set of birds exhibits high fecundity and another low fecundity it is to be understood that both sets were hatched, reared, fed and cared for in all respects in as nearly precisely the same way as is possible, considering that fowls are, in some degree, free agents and cannot be absolutely controlled. The extent both in time and space, and the manifoldness in respect to method, of the experiments upon which this discussion is based are so great and the checks on this point have been so numerous as to make it quite certain that the results are not influenced by a differential effect of the environment, arising from individual preferences of birds for particular sorts of food, or other similar peculiarities of behavior. When a result is stated to be due to inheritance the reader may assume, even though a specific statement is not made to that effect, that careful, critical consideration has been given to possible environmental influences.

This physiological complex may be designated as the 'excess production' factor in fecundity.

We may next consider in greater detail these factors influencing fecundity, taking first

The Anatomical Basis of Fecundity

Since, as already pointed out, egg production obviously depends in part upon the presence of ova in a normal ovary, a question which demands consideration is the following:

To what extent are observed variations in fecundity (i. e., in the number of eggs laid) to be referred to anatomical differences? In other words, does the ovary of a high producing hen, with for example, a winter record of from 75 to 115 eggs, contain a larger number of oöcytes than does the ovary of a hen which is a poor producer, laying no eggs in the winter period and perhaps but 10 or 15 eggs in the year?

To get light upon this question the observations to be described have been made. The object was to arrive at as accurate a relative judgment as possible regarding the number of oöcytes in the ovaries of different individual birds. It is, of course, impossible practically to determine accurately the total absolute number of oöcytes in the ovary. What can be done, is to count the number of oöcytes which are visible to the unaided eye. While such results do not tell us, nor enable us to estimate with great accuracy, the total number of oöcytes in the ovary, they do nevertheless throw interesting and useful light on the question raised above.

The counts of the visible oöcytes for a number of birds are given in table 4. These counts were made at my suggestion by my assistant, Miss Maynie R. Curtis, to whose painstaking care and skill in carrying through the tedious business of counting it is a pleasure to acknowledge gratefully my indebtedness. Prof. W. F. Schoppe of the University of Maine is carrying this work forward and later we hope to be able to publish more extensive data. So far as I am aware the counts here given are the first attempt yet made at anything more than the roughest sort of a guess at the number of eggs in a bird's ovary. While

these counts do not give the total numbers they do establish minimum values. A given ovary certainly does not carry any less than the number of visible ova.

A word should be said as to the method of making the counts, and the meaning of the subdivisions of the table. The counts were made in some cases on fresh, and in other cases on preserved ovaries. There was found to be little difference in the two methods, as regards the ease and accuracy of counting. In making the counts small pieces of ovary were cut off, and teased apart with needles under water and the visible oöcytes on the small fragments counted. In delimiting boundaries where a number of small oöcytes were closely packed together, a hand lens was used. No oöcyte was counted, however, which could not be seen with the unaided eye. In other words the lens was not used to find oöcytes which might otherwise be missed, but merely to aid in the dissecting of the material.

In the oöcyte counts given in the table it will be noted that these are grouped into four categories. The first class includes ruptured follicles from which the ova have been discharged. A ruptured follicle which is large at the moment the ovum leaves it gradually shrinks in size and is more or less completely absorbed. On the ovary of a hen which has laid, however, there will always be found a certain number of these discharged follicles not yet absorbed. When such follicles get very small it is exceedingly difficult to distinguish them from small oöcytes (i. e., undischarged follicles). Undoubtedly there are errors in classification in this respect in the counts, but for present purposes this is not a matter of great importance. If the eye were sharp enough it might perhaps be possible to distinguish a ruptured follicle for every egg which has ever been laid, since it is doubtful if the absorption is ever so complete as to leave absolutely no scar. It is of interest to note that in the counts there is a reasonably close relation between the follicle count and the record of eggs laid.

The oöcytes proper are divided in the counting into three classes: those 1 cm. or over in diameter, those between 1 mm. and 1 cm. in diameter, and those less than 1 mm. in diameter. The first of these classes includes the large yolks nearly ready to leave the ovary and pass into the oviduct. They are in pro-

TABLE 4

Showing the number of visible oöcytes in the ovary of certain birds

Case No.	Bird No.	Breed.	Date of Hatching.	Date Killed.	Total number of eggs laid in life.	Winter production.	Discharged follicles.	Oöcytes 1 cm. or over in diameter.	Oöcytes 1 mm. to 1 cm. in diameter.	Oöcytes under 1 mm. in diameter.	Total visible oöcytes.
1	8021	Barred Ply. Rock	June 1, '10	March 28, '11	10	3	17	9	53	1149	1228
2	8017	Barred Ply. Rock	June 2, '10	March 30, '11	10	0	12	7	51	1596	1666
3	8030	Barred Ply. Rock	June 1, '10	March 10, '11	7	0	8	5	62	837	914
4	8005	Barred Ply. Rock	June 2, '10	March 14, '11	17	5	12	8	68	1096	1174
5	1367	Barred Ply. Rock	April 28, '10	April 4, '11	34	3	49	7	29	2121	2306
6	8018	Barred Ply. Rock	June 2, '10	March 24, '11	16	0	23	6	42	1123	1194
7	8009	Barred Ply. Rock	June 2, '10	March 24, '11	15	0	17	6	49	2029	2101
8	8010	Barred Ply. Rock	May 19, '10	March 17, '11	19	5	24	5	92	1455	1576
9	425	Barred Ply. Rock	March 30, '09	July 7, '10	23	0	21	12[1]	142	1346	1521
10	3546	White Leghorn[2]	May 18, '09	December 20, '10	198	54	75	[3]	231	2146	2452
11	2067	White Leghorn	May 28, '09	December 15, '10	197	32	217	1	108	3279	3605
12	3453	White Leghorn	May 21, '09	December 13, '10	10	0	11	[3]	75	1626	1701
13	3833	White Leghorn	June 14, '09	December 22, '10	2	0	43	[3]	80	2022	2145
14	52	Cornish Ind. Game	April 21, '09	July 12, '10	52	13	54	6	167	1323	1550
15	71	Ft Cross	March 31, '10	March 20, '11	124	106	50	5	70	1875	2000
16		Guinea hen	?	January '11	?		9	3	36	717	765
17		Guinea hen	?	January '11	?			3	38	545	586

[1] This includes 8 yolks in process of absorption.

[2] For this and the three following birds I am indebted to Prof. James E. Rice of Cornell University, who very kindly gave me these trap-nested individuals for use in the present study. The egg records in these cases are not the records for life, but the records up to November 1, 1910. The figures represent practically the total production.

[3] Birds not in laying condition when killed.

cess of rapid enlargement by the deposition of yolk. The next class includes those oöcytes in which yolk deposition is started but is proceeding at a slow rate. It is from this class that the first class of rapidly growing yolks is constantly being recruited. Finally the "under 1mm." class represents the make-up of the bulk of the ovary. It will be understood that these size classes are only roughly delimited, the diameter of each oöcyte having been estimated but not carefully measured.

Columns in the table are devoted to "Total number of eggs laid in life" and "Winter production." The first of these has no particular significance since obviously it depends on when the bird was killed in order to make the oöcyte count. Winter production, however, represents a definite entity in fecundity as already pointed out above (p. 292).[6] Winter production records are directly comparable with one another. It is the inheritance of this fecundity unit that is primarily being studied in these investigations.

From this table a number of points are to be noted. In the first place it is clear that the number of visible oöcytes in the ovary of a hen is very large: much larger, I think, than has generally been supposed. While to be sure there are for the most part only vague statements respecting this point in the literature, usually these statements are to the effect that the birds ovary contains 'several hundred' ova. The only direct statement as to the actual number of oöcytes in a hen's ovary which I have been able to find is given by Matthews Duncan (8) on the very dubious authority of Geyelin (11) to the following effect (loc. cit., p. 36): "It has been ascertained that the ovarium of a fowl is composed of 600 ovula or eggs: therefore, a hen during the whole of her life cannot possibly lay more eggs than 600, which in a natural course are distributed over nine years in the following proportion." This statement is followed by an utterly preposterous and presumably entirely imaginary table from Geyelin, supposed to show the laying of hens at different ages. How far from the truth the table is is indicated

[6] For general discussion of "winter production" as a unit of fecundity, see (28), (30), (34), (37), (38). It comprises the egg production up to March 1 of the laying year.

by the fact that according to it the pullet year is the least productive of any of a hen's life, save only for the ninth year when the last remnants of the original 600 eggs are being tardily and, one must suppose, sorrowfully ejaculated!" As a matter of fact repeated trap-nest and other tests in all parts of the world have shown again and again that, on the average, the pullet year is the most productive of a hen's life.

From the figures given in table 4 it is furthermore apparent that the absolute number of oöcytes in the hen's ovary is very much larger than the number of eggs which any hen ever lays. A record of 200 eggs in the year is a high record of fecundity for the domestic fowl, though in exceptional cases it may go even a hundred eggs higher than this (cf. 29). But even a 200-eggs record is only a little more than a tenth of the average total number of visible oöcytes in a bird's ovary, to say nothing of the probably much larger number of oöcytes invisible to the unaided eye, but capable of growth and development. In other words it is quite evident from these figures that the potential 'anatomical' fecundity is very much higher than the actually realized fecundity. This is true even if we suppose the bird to be allowed to live until it dies a natural death. Experience shows that birds which make a high fecundity record in the first year of their life, generally speaking, never do so thereafter. In general an examination of what long period records are available in the statistics of this Station, and also in the literature, indicates that probably only relatively few birds of the American or Asiatic breeds at least, would lay many more than 400 to 500 eggs in their natural life time, if they were allowed to live it out. Records of '1000-egg' birds are in existence, but such birds are rare.

One of the longest continuous egg records of an individual bird, which may be considered accurate, with which I am acquainted is that given by Handrik (15) (for a Leghorn). This bird was hatched in 1901. Its egg record was as follows:

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[7] It is difficult to understand how so acute an investigator as F. H. A. Marshall could have been so imposed upon by this wonderful table of Geyelin's as to republish it in his valuable and interesting book on the "Physiology of Reproduction."

Calendar year	*Eggs laid*
1902	105
1903	163
1904	138
1905	159
1906	160
1907	133
1908	111
Total	969
Average per year	138 3-7

Heier (17) gives a four-year record for a Braekel hen, which is distinctly higher than would usually be obtained over so long a period. The figures are as follows:

Laying Year	*Eggs laid*
First	153
Second	139
Third	152
Fourth	162
Total	606
Average per year	151 1-2

In this connection the paper of Dackweiler (5) is of interest. Both of the cases here cited are of fowls of the Mediterranean type, in which the tendency to accumulate body fat with advancing age is not marked. I know of no records comparing with these in extent for Plymouth Rocks or other American or Asiatic breed. After two years the fecundity of Plymouth Rocks, in all cases which have been observed at the Maine Experiment Station, becomes greatly reduced.

An examination of table 4 in detail indicates that there is no very close or definite relationship between the number of visible number of oöcytes on the ovary and the winter production of a bird. Thus no. 1367 and no. 3546 each have about the same number of visible oöcytes, yet one has a winter production record 18 times as great as the other. Again no. 71 with the extraordinarily high winter record of 106 eggs has only a little more than one-half as many visible oöcytes as has no. 2067, whose winter production record is only 32 eggs. Again no. 71 with its 106 record has very nearly the same oöcyte count as no. 8010 with a winter record of zero. In general it may be said that the present figures give no indication that there is any correlation between fecundity as measured by winter production, and the number of oöcytes in the ovary. Of course, the

present statistics are meager. More ample figures are needed (and are being collected) from which to measure the correlation between actual and 'anatomical' fecundity.

But the data now in hand, even at the very lowest valuation which may be placed upon them, indicate clearly, it seems to me, that there must be some other factor than the anatomical one involved in the existence of different degrees of actual fecundity in the domestic fowl. It clearly is the case from table 4 that when one bird has a winter record of twice what another bird has it is *not* because the first has twice as many oöcytes in the ovary. On the contrary it appears that all birds have an anatomical endowment entirely sufficient for a very high degree of fecundity, and in point of fact quite equal to that possessed by birds which actually accomplish a high record of fecundity. Whether or not such high fecundity is actually realized evidently depends then upon the influence of additional factors beyond the anatomical basis. As has already been indicated in the preceding section it is reasonable to suppose that these factors are physiological in nature. The record of hen no. 71 shows most clearly and distinctly the reason why we must assume that there are definite physiological factors at work in determining relative degrees of fecundity, as measured by winter production.

While there are no oöcyte counts yet available for wild birds it is possible that when made they will show the same point as is here brought out, namely that there is no close or definite relation between the anatomical endowment and actually realized fecundity. In this connection a statement made by Jenner (20) a century and a quarter ago regarding the cuckoo is of interest. He says:

That the cuckow actually lays a great number of eggs, dissection seems to prove very decisively. Upon a comparison I had an opportunity of making between the ovarium, or racemus vitellorum, of a female cuckow, killed just as she had begun to lay, and of a pullet killed in the same state, *no essential difference appeared.*[8] The uterus of each contained an egg perfectly formed and ready for exclusion; and the ovarium exhibited a large cluster of eggs, gradually advanced from a very diminutive size to the greatest the yolk acquires before it is received into the oviduct.

[8] Italics not in original.

The Mechanism of the Inheritance of Fecundity

With so much by way of introduction we may proceed to the subject in hand, namely a detailed account of the manner in which fecundity is inherited. In this account for reasons which have been stated above, and in earlier papers on this subject, attention will be confined to winter egg production.

A. Observed types of winter egg production. A study of numerous statistics shows that hens fall into three well defined classes in respect to winter production. These classes include (*a*) those birds which lay no eggs whatever in the winter period (up to March 1 of the laying year); (*b*) those that lay but have a production during the period of something under about 30 eggs; and finally (*c*) those whose production exceeds 30 eggs in the winter period. The division point between classes (*b*) and (*c*) is not sharply defined in every case, but it is plainly (as will appear later) at about 30 eggs. Since in the analysis some fixed point must be taken for this boundary a production of 30 has been chosen for this purpose and will be used throughout. This is an arbitrary choice only in the sense that it is a convenient round number lying near where the biological division point falls, at least in the strains of domestic fowls used in these experiments. The analysis could doubtless be carried through nearly or quite as well by taking the division point at a production of 29 or 31, but 30 is a more convenient figure.

In making the division of winter egg production into three groups it must be remembered that this is a character subject to purely somatic fluctuations and environmental influence. Allowance for these factors must be made in interpreting and classifying results. In particular the following points must be kept in mind throughout.

(1) A zero winter production may be due to genetic causes or to purely somatic (physiological) ones, and there is nothing in a single record of this sort, taken by itself, to indicate to which category it belongs. A bird may carry the factor or factors for winter production, yet owing to purely physiological causes, such as a disturbance of metabolism, or of the ovary in respect to its physiology, or to disease, patent or obscure, it may never actually lay during the winter period. Usually it will be possible to tell from other considerations than the record itself, whether a given zero record is 'somatic' or 'genetic.'

(2) The upper limit of the winter period at March 1 is arbitrary, and only approximately coincides with the biological reality. Actually with most birds the spring or reproductive cycle of production (cf. 37) begins in the latter part of February. In handling the material it has been found necessary (for reasons which will be obvious upon consideration of the matter) to take a fixed date for the beginning of the spring cycle of laying and the ending of the winter cycle. The records of the Station prior to 1908 are tabulated only for months (the daily records unfortunately having been destroyed before I took charge of the work), and on this account it is necessary to take the working limit of the winter cycle at the end of a calender month. Since March 1 comes the nearest to the biological limit of any date which is also the beginning of a calendar month it has been chosen. The error introduced by taking this arbitrary date for a point which really shifts within rather narrow limits is, on the average, small. However, it must be recognized as a disturbing element in the individual case. Thus, some birds which really lack any genetic factor for winter production will begin to lay in the last days of February, and consequently on the arbitrary 'March 1' basis will actually be credited with a small winter production. This will tend to make the number of zero birds observed smaller than that expected on theory.

(3) Owing to the factors of environmental influence and somatic fluctuations it is difficult to classify birds in respect to fecundity, which have winter records near the boundary point, 30 eggs. Some birds bearing genes for a production of under 30 eggs will actually lay 31, or 32, or 33, etc. The point considered under (2) again comes into play here. A bird may bear the genes for an 'Under 30' record, and actually make such a record during the true biological winter cycle or period. But if it begins the spring cycle early (i. e., before March 1) it gets credited on its winter record with the eggs which it lays in the last days of February, but which biologically belong with the spring production, and in this way its apparent winter record becomes something over 30, while its real winter production was under 30.

All these factors obscure and render difficult the critical classification and interpretation of the results. Allowance must be made for their influence.

B. Symbolic analysis. After some consideration it has seemed advisable to undertake the presentation of what is at best a complicated matter in the following order. First a symbolic analysis of the inheritance of winter egg production will be given. Then the actual statistics of production covering a period of four years will be given, and it will be shown that these objective data are in substantial accord with the symbolic account. The facts can be presented in this way much more clearly and simply, than if the reverse order is followed. Without the clue of the symbolic analysis to guide one through the maze of figures, one would be hopelessly lost. It scarcely needs to be said that while the order suggested seems undoubtedly the best for the presentation of the results, it is precisely the opposite of that by which the conclusions here set down were reached.

Let us turn to the symbolic analysis. As has been pointed out already there are to be distinguished, on purely biological grounds, three factors involved in fecundity in the female fowl. These are:

(1) An anatomical factor. This is basic. It consists in the presence of a normal ovary, the primary organ of the female sex. In the following analysis a separate letter will not be used for the designation of this factor but instead it will be understood to be included in the letter denoting the presence of the female sex. That is, F will denote the presence of the female sex or its determiner, and the presence of the ovary. The letter f will denote presence of the male sex (the absence of the female sex determiner, from the symbolic standpoint) and the absence of an ovary. Obviously a separate letter is not needed for this 'anatomical factor' since the presence of an ovary is the objective criterion of the existence of the female sex, and its absence of the existence of the male sex.

(2) The first production factor. This is the primary physiological factor which in coexistence with F makes the bird lay eggs during the winter period. Quantitatively it may be taken as determining a winter production of more than zero eggs and less than 30. The presence of this factor will be denoted by L_1 and its absence by l_1

(3) The second production factor. This is a second physiological factor, which in coexistence with F and L_1 leads to

high fecundity. The presence of this factor will be denoted by L_2 and its absence by l_2. When F and L_1 are present the addition of L_2 makes a winter production of over 30 eggs. If F is present and L_1 absent (l_1) the presence of L_2 leads to a winter production of under 30 eggs. Thus either L_1 or L_2 alone makes a record of 30 eggs. They are independent determiners of this degree of production. It should be pointed out, however, that in spite of their equivalence in this regard, the factors L_1 and L_2 are not qualitatively the same. That is, the increased production when L_1 and L_2 are both present, is not because there are present two 'doses' of the same determiner. The proof of this is found in the fact that when there are two 'doses' of L_1 present in a bird it does not make her a high producer. L_2 may be considered an excess production factor, which erects a superstructure on the foundation furnished by L_1. In the absence of L_1 L_2 lacks the foundation from which to start and hence only can build about as high as L_1 would alone. One L_1 cannot, however, build a superstructure on another L_1; nor can an L_2 build one on another L_2. Of course it will be understood that with f (absence of female sex and ovary) these physiological fecundity factors L_1 and L_2 are simply latent.

Using the letters in the manner defined above, and with the usual Mendelian method of writing gametic and zygotic formulae, the data indicate the existence of Barred Plymouth Rock and Cornish Indian Game males and females of the constitutions set forth below. The only point needing particular attention in reference to these formulae is that the factor L_2 behaves in inheritance as a sex-limited character precisely like the barred color pattern of the Barred Rock (40, 41). In consequence gametes of the type FL_2 are never formed. Any gamete which bears F does not, under any circumstances, ever carry L_2.

It is not desirable to take the space to consider here all the consequences which flow from the circumstance of the high fecundity factor L_2 being a sex-limited character. These matters will be fully discussed farther on in the paper after the data themselves have been presented. Here it need only be said that since L_2 is a sex-limited character corresponding in behavior to the barred color pattern, it means that ♂ ♂ may be formed with any combination of the factors L_1 and L_2, whereas ♀ ♀ which bear L_2 at all, must be heterozygotic in respect to it. Females

may, however, be either homozygotic or heterozygotic in respect to L_1, it not being a sex-limited character, and hence not in any way coupled with or repelled by the factor *F*. That the female fowl is heterozygotic in respect to the sex factor was suggested by Spillman (50, 51) and has been demonstrated by the experimental studies of Bateson (3), Goodale (12, 13), Hagedoorn (14), Sturtevant (51) and Pearl and Surface (40, 41).

Tables 5 to 8 inclusive show the constitution in respect to fecundity of males and females of the breeds used in this work, as indicated by the results obtained from breeding experiments. These constitutions represent the 'Erbformeln which flow from the facts, and, in determination of their adequacy, are to be tested against the facts. In these tables the columns headed 'Gametes produced' have been made up in accord with the general Mendelian principle that in gametogenesis all possible com-

TABLE 5

Constitution of Barred Plymouth Rock males in respect to fecundity

Class	Zygote	Gametes Produced
1	fL_1L_2 . fL_1L_2	fL_1L_2
2	fL_1L_2 . fL_1l_2	fL_1L_2, fL_1l_2
3	fL_1L_2 . fhL_2,	fL_1L_2, fhL_2
4	fL_1L_2 . fhl_2	fL_1L_2, fL_1l_2, fhL_2, fhl_2
5	fL_1l_2 . fL_1l_2	fL_1l_2
6	fL_1l_2 . fhl_2	fL_1l_2, fhl_2
7	fhL_2 . fhL_2	fhL_2
8	fhL_2 . fhl_2	fhL_2, fhl_2
9	fhl_2 . fhl_2	fhl_2

TABLE 6

Constitution of Barred Plymouth Rock females in respect to fecundity

Class	Zygote	*f*-Bearing (♂ Producing) Gametes	*F*-Bearing (♀ Producing) Gametes	Probable Winter Egg Production of ♀ of Indicated Zygotic Constitution
1	fL_1L_2 . FhI_2	fL_1L_2, fhL_2[1]	FhI_2, FL_1I_2	Over 30 eggs
2	fL_1L_2 . FL_1I_2	fL_1L_2	FL_1I_2	Over 30 eggs
3	fL_1I_2 . FhI_2	fL_1I_2, fhI_2	FhI_2, FL_1I_2	Under 30 eggs
4	fL_1I_2 . FL_1I_2	fL_1I_2	FL_1I_2	Under 30 eggs
5	$f\ hI_2$. FhI_2	$f\ hI_2$	FhI_2	Zero eggs
6	$f\ hL_2$. FhI_2	$f\ hL_2$	FhI_2	Under 30 eggs

[1] The reason that gametes of the type fL_1I_2 and fhI_2 are not formed here will be evident on consideration. Since no gametes of type FL_2 can, by hypothesis, be formed this implies that an interchange of the factors L_2 and l_2 between *F* and *f* gametes cannot occur. The experimental proof of the truth of this conviction has been furnished in the case of the inheritance of the barred color pattern.

binations of the factors present will be formed, within the bounds of any limitation which may be imposed by such phenomena as coupling, repulsion or linkage. The limitation of these possibilities in the present instance has been set forth above: it consists simply in the fact that F and L_2 are never

TABLE 7

Constitution of Cornish Indian Game males in respect to fecundity

Class	Zygote	Gametes Produced.
1	$fL_1l_2 \cdot fL_1l_2$	fL_1l_2
2	$fL_1l_2 \cdot f\ l_1l_2$	fL_1l_2, fl_1l_2
3	$f\ l_1l_2 \cdot f\ l_1l_2$	$f\ l_1l_2$

TABLE 8

Constitution of Cornish Indian Game females in respect to fecundity

Class	Zygote	f-Bearing (♂ Producing) Gametes	F-Bearing (♀ Producing) Gametes	Probable Winter Egg Production ♀ of Indicated Zygotic Constitution
1	$fL_1l_2 \cdot FL_1l_2$	fL_1l_2	FL_1l_2	Under 30 eggs
2	$f\ l_1l_2 \cdot FL_1l_2$	$f\ l_1l_2, fL_1l_2$	FL_1l_2, Fl_1l_2	Under 30 eggs
3	$fL_1l_2 \cdot Fl_1l_2$	$fL_1l_2. fl_1l_2$	Fl_1l_2, FL_1l_2	Under 30 eggs
4	$f\ l_1l_2 \cdot Fl_1l_2$	$f\ l_1l_2$	Fl_1l_2	Zero eggs

It will be noted that C. I. G. ♀ classes 2 and 3 are gametically identical. Both are left in the table, however, since the whole table is so short that no confusion can be caused, and this example may make clear to some readers the nature of the compression (by omission of duplicate classes) which was practised in tables 5 and 6.

borne in the same gamete. It should be said that these tables do not show at all the proportions in which the several gametic types might be expected to occur. Further all duplicates have been omitted, so that only the different possible types are shown in these tables.

It will be noted from table 6 that two classes of females (1 and 2) carry both L_1 and L_2 and hence are to be expected, on the hypothesis developed, to be high layers. One class (class 5) carries neither L_1 nor L_2 and hence should make zero winter records. It should be said that observations indicate that while such class 5 birds occur with expected frequency, they usually do not produce any offspring. A zero winter layer usually gets very few chicks of any kind and almost never has any adult ♀ progeny.

Turning our attention to the Cornish Indian Games, we have the gametic constitutions set forth in tables 7 and 8. The only special point to be noted here is that the factor L_2 does not appear at all in either males or females. All the evidence indicates that in the strain of Cornish Indian Games used in these experiments, this excess production factor L_2 is entirely absent (cf. in this connection tables 1, 2 and 3, supra).

We may next consider the theoretical results which would be expected to follow the mating in all possible combinations of birds of the constitutions set forth above. In doing this account will be taken of female progeny *only*, for the sake of simplicity, saving of space, and because we are here concerned only with actual fecundity as expressed in the female. Anyone who desires can easily work out the ♂ constitutions for himself. Tables 9 and 10 give the expected numbers of female progeny from each mating, on the assumption of uniform fertility throughout. It will be seen that some old ratios should appear.

It should be pointed out that while, for the sake of completeness, the result of every possible mating is carried out in table 9 on an assumption of equal fertility for all matings, this by no means accords with actual fact. Certain of the matings would not in practice get any offspring at all. This applies also to table 10. This point will be made clear in connection with the application of the theoretical frequencies to the observed data.

It will not be necessary in the table for Cornish Indian Games to present the theoretical frequencies in such detail. Only totals and ratios will be given.

From table 10 it will be seen that no high layers are to be expected from pure Cornish Game matings and that further the proportion of zero layers is relatively high.

Analysis of the Experimental Data

In this section the actual results in respect to fecundity will be compared with the theoretical expectations. There will be presented first the data respecting the matings of Barred Rock males and females (pure B.P.R. matings); second the data respecting matings of Cornish Indian Game males and females (pure C.I.G. matings); and finally the F_1 and F_2 matings of Barred Plymouth Rocks and Cornish Indian Games crossed reciprocally.

TABLE 9

Showing the theoretical expectation in respect to the fecundity of the daughters from all possible matings of Barred Plymouth Rocks inter se

Matings.		Expected Distribution of Fecundity Among ♀ Progeny of the Designated Mating.			
B. P. R. ♂ of class	B. P. R. ♀ of class	Daughters with a winter production *over 30 eggs*		Daughters with a winter production of *under 30 eggs*	Daughters with a winter production of *zero eggs*
1	1 to 6 inclusive		32		
1	All classes	Ratio =	1	0	0
2	1		4	4	
2	2		2	2	
2	3		4	4	
2	4		2	2	
2	5		2	2	
2	6		2	2	
2	All classes	Totals =	16	16	
2	All classes	Ratio =	1	1	0
3	1		6	2	
3	2		4		
3	3		6	2	
3	4		4		
3	5		2	2	
3	6		2	2	
3	All classes	Totals =	24	8	
3	All classes	Ratio =	3	1	0
4	1		3	4	1
4	2		2	2	
4	3		3	4	1
4	4		2	2	
4	5		1	2	1
4	6		1	2	1
4	All classes	Totals =	12	16	4
4	All classes	Ratio =	3	4	1
5	1 to 6 inclusive			32	
5	All classes	Ratio =	0	1	0
6	1			6	2
6	2			4	
6	3			6	2
6	4			4	
6	5			2	2
6	6			2	2
6	All classes	Totals =		24	8
6	All classes	Ratio =	0	3	1
6	1			6	2
7	1		4	4	
7	2		4		
7	3		4	4	
7	4		4		
7	5			4	
7	6			4	
7	All classes	Totals =	16	16	
7	All classes	Ratio =	1	1	0
8	1		2	4	2
8	2		2	2	
8	3		2	4	2
8	4		2	2	
8	5			2	2
8	6			2	2
8	All classes	Totals =	8	16	8
8	All classes	Ratio =	1	2	1

TABLE 9—Continued

Matings.		Expected Distribution of Fecundity Among ♀ Progeny of the Designated Mating.			
B. P. R. ♂ of class	B. P. R. ♀ of class	Daughters with a winter production *over 30 eggs*		Daughters with a winter production of *under 30 eggs*	Daughters with a winter production of *zero eggs*
9	1			4	4
9	2			4	
9	3			4	4
9	4			4	
9	5				4
9	6				4
9	All classes	Totals =		16	16
9	All classes	Ratio =	0	1	1
All classes	All classes	Grand Total =	120	160	40
All classes	All classes	Ratio =	3	4	1

Since the actual breeding operations were carried out in advance of any understanding of the mechanism of the inheritance of fecundity the matings were substantially at random so far as concerns fecundity factors. As a consequence not all possible gametic pairings have been made, while for certain combinations a relatively large number of offspring are available. Enough of the possible gametic combinations have, however, been made with Barred Rocks to show clearly how fecundity is inherited.

A word should be said in regard to the number of offspring

TABLE 10

Showing the theoretical expectation in respect to the fecundity of the daughters from all possible matings of Cornish Indian Games inter se

Mating		Expected Distribution of Fecundity Among ♀ Progeny of the Designated Mating			
C. I. G. ♂ of class	C. I. G. ♀ of class	Daughters with a winter record of *over 30 eggs*		Daughters with a winter record of *under 30 eggs*	Daughters with a winter record of *zero eggs*
1	1 to 4 inclusive			12	
1	All classes	Ratio =	0	1	0
2	1 to 4 inclusive	Totals		9	3
2	All classes	Ratio =	0	3	1
3	1 to 4 inclusive	Totals		6	6
3	All classes	Ratio =	0	1	1
All classes	All classes	Grand totals		27	9
		Ratio =	0	3	1

from the different matings. The writer would, of course, be glad if records were at hand for a large number of progeny for every mating made. There are, however, practical difficulties in the matter. The Maine Agricultural Experiment Station poultry plant has accommodations for only about 600 adult pullets per annum in spite of the fact that it is one of the largest purely experimental poultry plants in the country.[9] Now taking all the experiments together there are made about 300 separate matings each year. It is simple arithmetic to show that under the circumstances, if all matings were equally represented, only two pullets from each mating could be tested as to fecundity. As a matter of fact all matings are not equally represented. Some yield either no chickens, or too few to insure the development of adult daughters. The aim has always been in this work to put into the laying house for trap-nest records of fecundity as many daughters from each one of as many matings as possible. Of course, only healthy, normal well developed pullets can be used in the work, since any other sort could not be depended upon to give reliable normal results as to fecundity. This means that, under the prevailing climatic conditions here, only pullets hatched between a rather narrow range of dates (April 1 to June 1) can be used in the fecundity. Those hatched at other seasons will not give normal results.

Altogether it will be seen that the character fecundity in fowls is not one which lends itself readily to treatment in large masses of figures, desirable as such might theoretically be. The case is very different from the study of the inheritance of plumage colors in poultry, for example, where both sexes are available for record and the records may be made while the chicks are relatively young (or in some cases even unhatched) and before they have time to die. If all students of the inheritance of pigmentation in poultry had been obliged to keep, house, and feed every bird which was to furnish any record whatever, until approximately one and a half years after hatching, and could have got records even then only from one sex (both of which conditions obtain in the study of fecundity), it is plain that their

[9] There are *hatched* annually on this plant from 3500 to 4000 chicks, and facilities for handling adult stock make it possible to accommodate over winter about 1000 birds of all sorts, including adult pullets, hens and male birds.

recorded numbers would have fallen very far below those which they have actually, and most fortunately for the good of biology, been able to obtain.

The foregoing remarks are not in any sense intended as an *apologia* for the statistical portion of this paper, because in the opinion of the writer, who is thoroughly acquainted with the practical difficulties which beset the study of inheritance of fecundity, no apology is needed. The data here presented are about as extensive as it is practically possible to obtain in an interval of time and with an experimental equipment equal to what has been available in the present investigation. It is hoped, however, that what has been said may help the reader, who may not be practically familiar with the rearing and trap-nesting of large numbers of fowls, to understand the reason why more extensive data are not forthcoming in this paper. In every case where the number of birds to a family was too small to warrant any conclusion this fact is particularly noted. The data for these small families are not suppressed, however, but are in most instances separately tabulated.

One convention which is used throughout in the tabulation of the material should be explained. In case a bird has a winter egg record of exactly 30 eggs, she evidently falls on the boundary line between the two fecundity classes already discussed and defined (p. 302). The number of such cases is not large, but in order to be perfectly impartial in their treatment it was decided to split such a bird in two, in a metaphorical sense, and credit one-half of her to the 'Over 30' winter fecundity class, and the other half to the 'Under 30' class. This explains the fractional records which occasionally appear among the frequencies in what follows, and which might otherwise puzzle one used to thinking of a hen as an individual unit, at least during the fecund portion of her existence. In calculating the mean winter production (in eggs) of the several classes these few birds with records of exactly 30 eggs have been omitted altogether. There are obviously two equally fair ways of dealing with them in getting these averages. One is to include each one in *both* 'over' and 'under' classes; the other is to include each one in *neither* class. The latter alternative is adopted because simpler.

Barred Plymouth Rock Matings

The data will be presented for each gametic constitution separately. The analysis indicates that out of the 9 theoretically possible types of male Barred Rocks shown in table 5 only six have actually ever been used in the breeding pens. These six classes of males represented in the data are classes 1, 2, 3, 4, 7 and 8.

In any particular case it is practicable to determine the gametic constitution of a male bird in respect to fecundity only through an examination of the records of his daughters. To distinguish different gametic types of males through analysis of the male progeny, while theoretically simply, is practically not feasible while any other investigations are going on. In order to determine the gametic constitution in regard to fecundity of the cockerels from a particular mating it would be necessary to rear to maturity a reasonable number (5 to 10) of these males, and then a year from the time they were hatched to mate each of them with a number of females, and rear to maturity and trap-nest for a year a number (3 to 10 for example) of pullets grown from each of the matings of each of the cockerels. Then from the trap-nest records of these pullets it would be possible to conclude as to what was their grandfather's gametic constitution respecting fecundity. It is evident that relatively enormous experimental resources would be required to carry this out on even a very modest scale. Further the end would scarcely justify the means from either a practical or theoretical standpoint, since the theoretically expected gametic types of males can be readily obtained and their pedigrees will enable one to analyze fully the gametic factors and reactions involved in their production.

Throughout the paper, then, conclusions will be drawn as to gametic constitution of parents from an analysis of the female progeny only.

The reason why the other three classes of males (5, 6 and 9) are not represented in the matings is to be found in the method of selective breeding practised during the time in which the statistics here analyzed were collected. The chance of using in a breeding pen males of any of these types was small when the selection was carried on in the way that it was. This point will be more fully discussed farther on in the paper.

Matings of Barred Plymouth Rock males of class[10] *7*

Males of class 7, having a gametic constitution fl_1L_2. fl_1L_2, were used more often than any other sort in the pure Barred Rock matings. They are homozygous with reference to the absence of the first production factor L_1, and the presence of the second or excess production factor L_2. A reference to table 9 shows that there should be no zero winter producers among their progeny. The proportions of high and poor layers in the progeny depend upon the nature of the female with which the male is bred. For convenience the matings of each individual male will be discussed separately.

B.P.R. ♂ 553. Indicated gametic constitution = fl_1L_2. fl_1L_2.

This male was hatched in the spring of 1908 and used as a breeder in the season of 1909. His successful 'pure' matings (i. e., those with B.P.R. females which produced adult female progeny) were as follows:

Matings: A. With 6 ♀ ♀ indicated to be of class 2=fL_1L_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	15	0	0
Expected	*15*	*0*	*0*
Mean winter production of ♀ ♀ in indicated class	51.33 eggs		

B. With 3 ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	6	9	0
Expected	*7.5*	*7.5*	*0*
Mean winter production of ♀ ♀ in indicated class	55.50 eggs	13.56 eggs	

C. With 2 ♀ ♀ indicated to be of class 4 = fL_1l_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	4	0	0
Expected	*4*	*0*	*0*
Mean winter production of ♀ ♀ in indicated class	39.75 eggs		

[10] The 'class' numbers throughout refer to the arbitrary designations given in tables 5 to 10 inclusive.

All ♀ Progeny

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	25	9	0
Expected	*26.5*	*7.5*	*0*
Mean winter production	50.48 eggs	13.56 eggs	

The agreement between observation and expectation here is as close as could be expected considering the numbers involved. Further it is evident from the mean production of the daughters falling in the several classes that the 'Over 30' and 'Under 30' classes are perfectly distinct in respect to degree of fecundity. The 'Over 30' birds produced on the average, nearly four times as many eggs in the winter period as the 'Under 30' birds.

B.P.R. ♂ 567. Indicated gametic constitution = fl_1L_2. fl_1L_2. This male was used in the breeding season of 1910 and sired a fairly large number of chicks of which the adult daughters appear below. He was hatched in the spring of 1909.

Matings: A. With 5 ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ Progeny

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	$7\frac{1}{2}$	$9\frac{1}{2}$	0
Expected	*8.5*	*8.5*	*0*
Mean winter production of ♀ ♀ in indicated class	57.28 eggs	14.78 eggs	

B. With 3 ♀ ♀ indicated to be of class 2 = fL_1L_2. Fl_1l_2.

♀ Progeny

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	12	2	0
Expected	*14*	*0*	*0*
Mean winter production of ♀ ♀ in indicated class	55.83 eggs	22.00 eggs	

C. With 2 ♀ ♀ indicated to be of class 6 = fl_1L_2. Fl_1l_2.

♀ Progeny

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	$1\frac{1}{2}$	$3\frac{1}{2}$	0
Expected	*0*	*5*	*0*
Mean winter production of ♀ ♀ in indicated class	48.00 eggs	14.00 eggs	

All ♀ Progeny

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	21	15	0
Expected	*22.5*	*13.5*	*0*
Mean winter production	55.95 eggs	15.64 eggs	

It will be noted that there are two exceptions in these matings. A class 7 ♂ × class 2 ♀ should give only daughters in the 'Over 30' class. Two out of the 14 adult progeny from matings of this type laid fewer than 30 eggs in the winter period. The record of one of these two was 28 eggs. There is no doubt that this bird was a somatic variation belonging gametically to the 'Over 30' class (cf. p. 302). In general it is obvious that the agreement between observation and expectation here is very satisfactory. Further the difference in average winter production of the birds in the 'Over 30' and 'Under 30' classes is so great as to leave no doubt of the real distinctness of these classes in respect to fecundity.

B.P.R. ♂ 562. Indicated gametic constitution = fhL_2. fhL_2.

This male got comparatively few adult daughters. He was used during only one breeding season (that of 1910), having been hatched in the spring of 1909.

Matings: A. With 4 ♀ ♀ indicated to be of class 1 = $fL_1L_2Fh_1l_2$.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	5	6	0
Expected	*5.5*	*5.5*	*0*
Mean winter production of ♀ ♀ of indicated class	42.40 eggs	11.67 eggs	

B. With 2 ♀ ♀ indicated to be of class 2 = fL_1L_2. Fhl_2

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	8	0	0
Expected	*8*	*0*	*0*
Mean winter production of ♀ ♀ of indicated class	70.00 eggs		

All ♀ Progeny

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	13	6	0
Expected	*13.5*	*5.5*	*0*
Mean winter production	59.38 eggs	11.67 eggs	

In spite of the comparatively small number of individuals here, the evidence of segregation of high and low fecundity in accordance with gametic expectation is clear and indubitable.

B.P.R. ♂ *552.* Indicated gametic constitution = fl_1L_2. fl_1L_2.

This male was used as a breeder during two seasons (1909 and 1910). He was hatched in the spring of 1908. His sisters were very poor winter layers, as shown by the following table.

Sisters of ♂ *552*	*Winter production as pullets* *Eggs*
E 184	16
E 229	6
E 272	7
Mean winter production of family	9.67

The mother of ♂ 552 (♀ D725) was a good layer with a winter record of 61 eggs. From her he evidently got an L_2 factor which his sisters could not acquire in this way. The father was heterozygous relative to L_2 (belonging to class 4) and the only one of his adult progeny from the mating with ♀ D725 to bear L_2 happened to be the ♂ 552 here under discussion. In the following account of ♂ 552's breeding history the progeny in both of the years in which he was used in the pens are taken together. There is no reason why the two years should be dealt with separately.

Matings: A. With 4 ♀ ♀ indicated to be of class 2 = fL_1L_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	11½	½	0
Expected	*12*	*0*	*0*
Mean winter production of ♀ ♀ in indicated class	48.27 eggs		

B. With 10 ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	17	15	2
Expected	*17*	*17*	*0*
Mean winter production of ♀ ♀ in indicated class	54.71 eggs	12.47 eggs	0 eggs

C. With 3 ♀ ♀ indicated to be of class 3 = fL_1l_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	2	1	0
Expected	*1.5*	*1.5*	*0*
Mean winter production of ♀ ♀ in indicated class	35.50 eggs	22.00 eggs	

All ♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	30½	16½	2
Expected	*30.5*	*18.5*	*0*
Mean winter production	51.07 eggs	13.06 eggs	0 eggs

In this case the two zero birds are without much question to be reckoned as somatic rather than genetic zeros. Unfortunately neither of these birds were bred, so that precise information on the point is lacking. Assuming this to be the case the agreement between observation and expectation in the large progeny is perfect. The matings under C got so few ♀ progeny as to be without significance one way or the other.

The mean winter productions again show the distinctness of the separation between the 'Over 30' and 'Under 30' fecundity classes.

B.P.R. ♂ *554.* Indicated constitution = fhL_2. fhL_2.

This bird, like ♂ 552 was used in the breeding pens two years. He was hatched in 1908 and bred in each of the two following years. His breeding history was as follows:

Matings: A. With 8 ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	12	12	1
Expected	*12.5*	*12.5*	*0*
Mean winter production of ♀ ♀ in indicated class	47.67 eggs	15.58 eggs	0 eggs

B. With 3 ♀ ♀ indicated to be of class 2 = fl_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	8	0	0
Expected	*8*	*0*	*0*
Mean winter production of ♀ ♀ in indicated class	59.00 eggs		

C. With 2 ♀ ♀ indicated to be of class 6 = fl_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	0	3	0
Expected	*0*	*3*	*0*
Mean winter production of ♀ ♀ in indicated class		20.33 eggs	

All ♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	20	15	1
Expected	*20.5*	*15.5*	*0*
Mean winter poduction	52.20 eggs	16.53 eggs	0 eggs

Barring the single bird with a zero record the agreement between observation and expectation here is perfect. This exception was a late[11] hatched bird (June 2, 1910). It laid an egg on May 1, 1911, of its pullet year, and died from a combination of pulmonary and intestinal difficulties on May 22. Under these circumstances it obviously carries little weight as an exception to expectation on a gametic basis.

B.P.R. ♂ 564. Indicated constitution = fl_1L_2. fl_1L_2.

This bird was hatched in 1909 and used in the breeding season of 1910, with the following results:

[11] It must always be remembered that 'late' is relative. Under our conditions of climate, etc., at Orono, June 2 represents very late hatching for birds which are to be used in fecundity work. The cold weather comes on so early in the fall and is so severe that any bird not fully developed by the middle of October or the first of November at the latest is likely to remain permanently stunted. The first of June represents about the latest possible limit of hatching for fecundity work under these conditions.

Matings: A. With 6 ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	9	10	2
Expected	*10.5*	*10.5*	*0*
Mean winter production of ♀ ♀ in indicated class	64.44 eggs	19.80 eggs	0 eggs

B. With 3 ♀ ♀ indicated to be of class 3 = fL_1l_2. Fl_1 l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	2	2	0
Expected	*2*	*2*	*0*
Mean winter production of ♀ ♀ in indicated class	54.50 eggs	26.50 eggs	

C. With 1 ♀ indicated to be of class 6 = fl_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	0	2	0
Expected	*0*	*2*	*0*
Mean winter production of ♀ ♀ in indicated class		4.00 eggs	

All ♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	11	14	2
Expected	*12.5*	*14.5*	*0*
Mean winter poduction	62.64 eggs	18.85 eggs	0 eggs

The families are small in this case. From both these pure Barred Rock and the cross matings in which ♀ 564 entered, however, there can be no doubt that he is a class 7 male. The two zero birds are to be reckoned as 'somatic zeros' rather than gametic. Both began laying at the very beginning of the spring period, and made records which indicated to one familiar with this sort of material that they belonged genetically in the 'Under 30' class and only by accident failed to lay some eggs during the winter period.

B.PR. ♂ *D58.* Indicated constitution = fhL_2. fhL_2.

This bird was purchased in January, 1908, from Gardner & Dunning, a then well-known firm of Barred Rock breeders of Auburn, N. Y. Nothing was known of this bird's previous history or pedigree. The bird was hatched in the spring of 1907, and used in our breeding pens in 1908 and 1909. In 1908 he failed to get any adult daughters. This, however, was not the fault of the bird, but of the conditions under which the breeding had to be done that year (cf. Pearl and Surface 35). From the records of the daughters of ♂ 58 obtained in 1909 and exhibited below it appears clear that he was a class 7 male. The breeding history is as follows:

Matings: A. With 9 ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	10	13	1
Expected	*12*	*12*	*0*
Mean winter egg production of ♀ ♀ in indicated class	52.22 eggs	17.25 eggs	0 eggs

B. With 4 ♀ ♀ indicated to be of class 6 = fl_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	0	5	0
Expected	*0*	*5*	*0*
Mean winter egg production of ♀ ♀ in indicated class		15.80 eggs	

All ♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	10	18	1
Expected	*12*	*17*	*0*
Mean winter production	52.22 eggs	16.82 eggs	0 eggs

The single zero bird here (♀ F158) cannot fairly be regarded as a non-conformable case because of the following history. She was hatched March 30, 1909. She never laid an egg and died May 23, 1910. Autopsy showed the ovary and oviduct to be in an infantile condition. The ovary weighed 1 gram and the oviduct 2 grams. The ovary showed no oöcytes enlarged by

yolk deposition or enlarging. There was no evidence that the ovary had ever shown the slightest trace of functional activity. But a *normal* bird hatched in March will exhibit signs of ovarian activity before May of the following year, even though she belongs genetically to the 'Zero' class in respect to winter production and does not lay. While the autopsy showed no obvious lesion of ovary or oviduct, this by no means proves that there may not have been present some deep-seated functional derangement.

B.P.R. ♂ *573.* Indicated constitution = $fl_1L_2.fl_1L_2$.

This bird was used in the breeding season of 1910, having been hatched in 1909. He proved not to be all that might be desired as a breeder, being somewhat lacking in vigor of constitution. Partly on this account, he got comparatively few adult daughters, as indicated in the following breeding history.

Matings: A. With 5 ♀ ♀ indicated to be of class 1 = $fL_1L_2.\ Fl_1l_2$.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	4½	6½	0
Expected	*5.5*	*5.5*	*0*
Mean winter production of ♀ ♀ in indicated class	47.50 eggs	15.67 eggs	

B. With 2 ♀ ♀ indicated to be of class 2 = $fL_1L_2.\ FL_1l_2$.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	4	0	0
Expected	*4*	*0*	*0*
Mean winter production of ♀ ♀ in indicated class	49.25 eggs		

C. With 1 ♀ indicated to be of class 3 = $fL_1l_2.\ Fl_1l_2$.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	2	1	1
Expected	*2*	*2*	*0*
Mean winter production of ♀ ♀ in indicated class	55.50 eggs	16.00 eggs	0 eggs

All ♀ Progeny

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	10½	7½	1
Expected	*11.5*	*7.5*	*0*
Mean winter production	49.80 eggs	15.71 eggs	0 eggs

The zero bird here is an exception for which no apparent explanation is forthcoming. She was not pathological. She was however a June hatched bird. Unfortunately she was not bred, and therefore it is not possible to be sure of her gametic constitution. In spite of the fact that the total number of progeny here is small, there is little doubt of the correctness of the classification.

The mean productions for birds in the 'Over 30' class in the several matings are comparatively a little lower than those of the progeny of other class 7 males. It is interesting to speculate as to whether this may be connected with the lack of great vigor on the part of the sire. No data are available from which to get critical evidence on this point.

B.P.R. ♂ 56. Indicated constitution = fl_1L_2. fl_1L_2.

This bird was purchased in January, 1908, from Mr. C. H. Welles of Stratford, Conn. It came from a strain of Barred Rocks well known in the show-room, but not specially bred for egg production. This fact is of interest in connection with the breeding history of the bird, which indicates clearly that he was homozygous with respect to L_2. The result shows, in other words, that a male Barred Rock from a strain bred purely for the fancy may still carry in pure form the factor for high egg production.

This male bird (56) was bred two seasons (1908 and 1909). The first year he got but very few adult daughters, owing to the unfavorable conditions under which all the breeding had to be done in 1908 (cf. Pearl and Surface 35.) In 1909 the results were better. The adult daughters from both seasons are taken together in the following breeding history.

Matings: A. With 5 ♀ ♀ indicated to be of class 2 = fL_1L_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	7	0	0
Expected	*7*	*0*	*0*
Mean winter production of ♀ ♀ in indicated class	54.57 eggs		

B. With 4 ♀ ♀ indicated to be of class 3 = fL_1l_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	9	4	0
Expected	*6.5*	*6.5*	*0*
Mean winter production of ♀ ♀ in indicated class	56.89 eggs	19.50 eggs	

C. With 2 ♀ ♀ indicated to be of class 6 = fl_1L_2 Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	0	3	0
Expected	*0*	*3*	*0*
Mean winter production of ♀ ♀ in indicated class		13.67 eggs	

All ♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	16	7	0
Expected	*13.5*	*9.5*	*0*
Mean winter production	55.87 eggs	17.00 eggs	0 eggs

The agreement between observation and expectation here is satisfactory, excepting the case of the class 3 females. There the deviation from the expected half is wide, but the numbers involvel are small. The behavior of ♂ 56 with class 2 and class 6 females gives clear indication of his gametic constitution.

B.P.R. ♂ *563.* Indicated constitution = fl_1L_2. fl_1L_2.

This bird was hatched in 1909 and used as a breeder in 1910. He was an exceptionally fine, vigorous bird. The breeding history is as follows:

Matings: A. With 6 ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	11	11	1
Expected	*11.5*	*11.5*	*0*
Mean winter production of ♀ ♀ in indicated class	64.09 eggs	17.91 eggs	0 eggs

B. With 5 ♀ ♀ indicated to be of class 2 = fL_1L_2 FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	18	1	0
Expected	*19*	*0*	*0*
Mean winter production of ♀ ♀ in indicated class	63.56 eggs	1.00 eggs	

All ♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	29	12	1
Expected	*30.5*	*11.5*	*0*
Mean winter production	63.76 eggs	16.50 eggs	0 eggs

Aside from the two outstanding exceptions the agreement between observation and expectation is excellent. From the records available there is no evident explanation for the two exceptions (the 'Zero' bird in the A matings, and the 'Under 30' bird in the B matings). Neither of the birds were bred, and hence no help is to be had from the progeny in explaining them. It is reasonable to suppose that the observed records for these birds are somatic fluctuations, but this cannot be demonstrated now. This case illustrates an unavoidable difficulty which attends that method of work which first collects data at random and without any theoretical guide, and then later undertakes their analysis. If one had been carrying on the breeding in the present case under the guidance of the hypothesis as to the mechanism of the inheritance of fecundity now under discussion, obviously many matings which actually were not carried out would have been made to test out somatically exceptional individuals and so learn their gametic constitution.

B.P.R. ♂ *D31.* Indicated constitution = fl_1L_2. fl_1L_2.

This rather remarkable bird was used as a breeder for three successive years, and then retired merely because no more of his progeny were needed, and not for any evident diminution of vigor on his part. This bird was first bred as a cockerel in the spring of 1908 (hatched in 1907). All that was known of his ancestry was that he was the son of a hen that had laid 200 or more eggs in her pullet year. Some notion of the vigor of ♂ D31 as a breeder may be gained from the fact that, taking all three seasons together and including all parts of the breeding season in each year, 89.4 per cent of all the eggs laid by hens mated with him were fertile. This is an extraordinarily high record considering all the circumstances, and particularly the seasonal and housing conditions. So far as concerns adult daughters the breeding history of this bird is as follows:

Matings: A. With 9 ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	10½	11½	0
Expected	*11*	*11*	*0*
Mean winter production of ♀ ♀ in indicated class	48.40 eggs	15.73 eggs	

B. With 8 ♀ ♀ indicated to be of class 2 = fL_1L_2 FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	27½	2½	0
Expected	*30*	*0*	*0*
Mean winter production of ♀ ♀ in indicated class	54.96 eggs	17.00 eggs	

C. With 8 ♀ ♀ indicated to be of class 3 = fL_1l_2 Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	14	15	1
Expected	*15*	*15*	*0*
Mean winter production of ♀ ♀ in indicated class	41.93 eggs	12.20 eggs	0 eggs

D. With 1 ♀ indicated to be of class 4 = fL_1l_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	5	0	1
Expected	*6*	*0*	*0*
Mean winter production of ♀ ♀ in indicated class	39.40 eggs		0 eggs

All ♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	57	29	2
Expected	*62*	*26*	*0*
Mean winter production	48.16 eggs	13.81 eggs	0 eggs

Besides the families noted above ♂ D31 got one adult daughter by each of two other females. Both these daughters had a winter record of zero eggs and were apparently pathological. In any event it was impossible to form any judgment as to their gametic constitution or that of their dams.

The general agreement between observation and expectation in this large progeny group is clear. The apparent exceptions to gametic expectation need some discussion. In the B matings (class 2 ♀ ♀) the record shows 2 1-2 in the 'Under 30' class where none is expected. Actually out of the 30 individuals from these matings only *one* daughter laid fewer than 30 eggs in the winter period. There were, however, 3 individuals which laid exactly 30 eggs in this period. So, in accordance with the convention adopted at the beginning, the record of 2 1-2 is made up as follows: 1 + 1-2 + 1-2 + 1-2 = 2 1-2. The one bird under 30 with a record of 17 eggs was late hatched and probably represented a somatic fluctuation. This bird was bred, but unfortunately got no offspring. Her eggs were nearly all fertile but the embryos died during incubation.

Of the two birds with a zero winter record it may be said that one (E96) was pathological, and on that account failed to lay. The autopsy on this bird, which died April 13, 1909, showed that it must have been functionally deranged for a long time preceding death. Yet there was clear evidence of functional activation of ovary and oviduct at some time before death. In this case the bird without question carried either L_1 or L_2 (or

possibly both) and the reproductive system started to function in the normal way and bring to somatic expression these gametic factors. But before this could be done the diseased condition of the organs brought the bird as a whole into such a condition of reduced vitality that egg production was impossible.

The other bird's zero record is probably a somatic fluctuation from an 'Under 30' hereditary constitution. She began laying very shortly after the end of the winter period.

It is of interest to note that the mean winter productions are relatively rather low for the 'Over 30' classes in all matings. The contrast between ♂ D31 progeny and that of ♂ 563 (vide supra) in this respect is striking. This matter will be discussed in detail later.

Summary and discussion of matings of class 7 Barred Plymouth Rock males. Having now presented in detail the evidence respecting the matings of class 7 males with various types of females it is desirable to collect and summarize this material. In tables 11 to 16 inclusive are given the assembled results of all matings of certain particular types. It will be understood that these are all pure Barred Rock matings and represent the summation of the data previously given. These tables give the total numbers of different males and females from which data were obtained in each class of matings, as well as the classification of the adult female progeny in respect to fecundity.

TABLE 11

Showing the results of all matings of class 7 ♂ ♂ × class 1 ♀ ♀
$fl_1L_2 \cdot fl_1L_2 \times fL_1L_2 \cdot Fl_1l_2$

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Adult Daughters.				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ offspring
10	75	Observed	92½	103½	7	203
		Expected	*101.5*	*101.5*	*0*	
Mean winter egg production of all daughters in designated class....			54.19 eggs	15.52 eggs	0 eggs	

TABLE 12

Showing the results of all matings of class 7 ♂ ♂ × class 2 ♀ ♀

fl_1L_2 . $fl_1L_2 \times fL_1L_2$. FL_1l_2

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Adult Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ offspring
9	38	Observed	111	6	0	117
		Expected	*117*	*0*	*0*	
Mean winter egg production of all daughters in designated class....			56.47 eggs	20.33 eggs		

TABLE 13

Showing the results of all matings of class 7 ♂ ♂ × class 3 ♀ ♀

fl_1L_2 . $fl_1L_2 \times fL_1l_2$. Fl_1l_2

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Adult Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ offspring
5	19	Observed	29	23	2	54
		Expected	*27*	*27*	*0*	
Mean winter production of all daughters in designated class.....			47.93 eggs	15.30 eggs	0 eggs	

TABLE 14

Showing the results of all matings of class 7 ♂ ♂ × class 4 ♀

fl_1L_2 . $fl_1L_2 \times fL_1l_2$. FL_1l_2

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Adult Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ offspring
2	3	Observed	9	0	1	10
		Expected	*10*	*0*	*0*	
Mean winter egg production of all daughters in designated class....			39.56 eggs		0 eggs	

TABLE 15

Showing the results of all matings of class 7 ♂♂ × class 6 ♀♀

$fl_1L_2 \cdot fl_1L_2 \times fl_1L_2 \cdot Fl_1l_2$

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Adult Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ offspring
5	11	Observed	1½	16½	0	18
		Expected	*0*	*18*	*0*	
Mean winter egg production of all daughters in designated class....			48.00 eggs[1]	14.44 eggs		

[1] The record of the single "Over 30" bird.

TABLE 16

Showing the results of all matings of class 7 ♂♂ with all classes of ♀♀

General Summary

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Adult Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ offspring
11	146	Observed	243.0	149.0	10	402
		Expected	*255.5*	*146.5*	*0*	
Mean winter egg production of all daughters in designated class....			53.67 eggs	15.37 eggs	0 eggs	

From these tables the following points would appear to be definitely established:

1. The numbers of different individuals used as parents in these matings and also the numbers of adult daughters obtained from them are great enough to give an adequate test of the hypothesis under discussion. In other words, we are not dealing here with the results of a few matings, and a small offspring series. One hundred and forty-six separate and distinct matings to test out males of one gametic constitution must be regarded as an adequate number.

2. *The evidence for a definite and clean-cut segregation of high fecundity and low fecundity in gametogenesis is clear and indubitable.* The expected proportions of high producers and low producers are closely realized in all the different types of matings.

3. Furthermore, the mean egg productions of the birds in the several gametic classes are widely separated, showing that the segregation is of perfectly distinct physiological entities. Refined biometric tests are not necessary to show that the birds carrying high fecundity hereditarily lay more than those with low fecundity hereditary factors. The birds in the 'Over 30' class have average winter productions *from three to five times* greater than those of birds belonging to the 'Under 30' class.

4. The agreement between observation and expectation for the several types of mating is as close as could be expected considering the nature of the material. The only discrepancy of note is caused by the 10 birds with zero records, where none are expected. In the detailed discussions in connection with each mating it has been shown, however, that nearly all of these 10 cases, when studied individually, have a physiological explanation, which makes it impossible to regard them as real exceptions to the gametic expectations. A determination might be made of the 'goodness of fit' of theory to observation by Pearson's (42) method, were it not for the fact that that method cannot be applied to cases like the present.[12]

[12] The difficulty lies in the fact that Pearson's test depends upon a variable

$$X_2 = S\left\{\frac{(m_r - m'_r)^2}{m_r}\right\}$$

where m_r is the theoretical frequency and m'_r the observed. Now obviously in any distribution where one m_r is zero, the value of X_2 must be infinity, whatever may be the values of the other m_r's or m'_r's. That is, if the theoretically expected frequency on any base element is numerically zero the probability against the whole curve becomes infinite. Thus, for example, suppose a system of frequencies like the following, a type which is continually arising in Mendelian work.

Class	1	2	3	4	5
Theoretically expected frequency...	595	827	68	0	96
Actually observed frequency	594	828	67	1	96

Now, it does not need a mathematical measure of any kind to tell one that in this case the theoretical and actual distributions are in very close agreement. Yet, because the *theoretical* frequency on class 4 is zero, the probability by Pearson's test is literally infinite *against* the observed distribution being regarded as a random sample of a population distributed in accordance with the theoretical frequencies. Pearson

Further discussion of various points brought out by these tables is deferred to a later section of the paper.

Matings of Barred Plymouth Rock males of class 4.

Males of class 4 have a gametic constitution fL_1L_2. fl_1l_2. That is, they are heterozygous with respect to both fecundity factors. Among the progeny are to be expected high, low and zero winter layers. Four male birds of this genotypic constitution have been used in the breeding experiments. Their records follow.

B.P.R. ♂ *569.* Indicated constitution = fL_1L_2. fl_1l_2.

This male was hatched in 1909, and bred the following year. His breeding history was as follows:

Matings: A. With 1 ♀ indicated to be of class 2 = fL_1L_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	2	0	0
Expected	*1*	*1*	*0*
Mean winter egg production of ♀♀ indicated class	67.00 eggs		

B. With 4 ♀♀ indicated to be of class 6 = fl_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	2	6	3
Expected	*2.75*	*5.5*	*2.75*
Mean winter production of ♀♀ in indicated class	75.00 eggs	7.33 eggs	0 eggs

(loc. cit., p. 164, footnote) had indeed himself noted what is essentially this same difficulty in using the test on ordinary frequency distributions.

The point noted obviously limits greatly the applicability of Pearson's test, and in a most unfortunate direction. Tests of goodness of fit are much needed in Mendelian work. But it is just here that classes where the theoretical frequency is zero often occur. To determine the probable error of the individual frequency in measuring the goodness of fit of Mendelian observation and theory, as was first practised by Weldon (52) and later by Johannsen (21) and by Mendelian workers generally, does not appear to the writer to be an altogether sound procedure. It fails to take account of the *correlations* in errors amongst the several frequencies. Yet these are just as important and just as certainly existent in a Mendelian 'category' type of distribution as in the ordinary variation polygon of a continuously variable character. This point I have alluded to elsewhere recently (Pearl, 32). Pearson's test covers this point, and were it not for the other difficulty noted above would be be much more widely useful in Mendelian work than is actually the case.

C. With 4 ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	5½	6½	1
Expected	*4.9*	*6.5*	*1.6*
Mean winter production of ♀ ♀ in indicated class	44.60 eggs	8.00 eggs	0 eggs

D. With 3 ♀ ♀ indicated to be of class 4 = fL_1l_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	3	3	0
Expected	*3*	*3*	*0*
Mean winter egg production of ♀ ♀ in indicated class	45.33 eggs	7.33 eggs	0 eggs

All ♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	12½	15½	4
Expected	*11.65*	*16*	*4.35*
Mean winter production	53.58 eggs	7.60 eggs	0 eggs

The agreement between observation and expectation is plainly very close here. The three fecundity classes are represented and in proportions as near to those indicated by hypothesis as could be expected, considering the numbers involved.

B.P.R. ♂ *566.* Indicated constitution = fL_1L_2. fl_1l_2.

This bird was used in the breeding pen in the season of 1910, having been hatched in the spring of the previous year. His sire was ♂ D556, a class 4 male to be taken up later, and his dam a class 2 female. His breeding history was as follows:

Matings: A. With 5 ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	4	8	2
Expected	*5.2*	*7*	*1.8*
Mean winter egg production of ♀ ♀ in indicated class	35.00 eggs	20.50 eggs	0 eggs

B. With 6 ♀ ♀ indicated to be of class 2 = fL_1L_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	9	6	0
Expected	*7.5*	*7.5*	*0*
Mean winter eggs production of ♀ ♀ in indicated class	50.44 eggs	11.83 eggs	0 eggs

All ♀ Progeny

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	13	14	2
Expected	*12.7*	*14.5*	*1.8*
Mean winter production	45.69 eggs	16.79 eggs	0 eggs

Here again the agreement between observation and expectation is very close, quite as close as could be expected with the numbers involved. The mean production of the 4 birds in the 'Over 30' class in the A matings is low.

B.P.R. ♂ D35. Indicated constitution = fL_1L_2. fl_1l_2.

This bird was one of the original males with which the present breeding experiments were started in 1908. The only thing known about his ancestry is that he was the son of a hen laying 200 or more eggs in the year. He got only a small adult female progeny, and was used as a breeder only one year. His breeding record follows.

Matings: A. With 4 ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	3	5	1
Expected	*3.4*	*4.5*	*1.1*
Mean winter production of ♀ ♀ in indicated class	58.67 eggs	15.20 eggs	0 eggs

B. With 2 ♀ ♀ indicated to be of class 3 = fL_1l_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	2	5	0
Expected	*2.6*	*3.5*	*0.9*
Mean winter production of ♀ ♀ in indicated class	37.50 eggs	14.60 eggs	

C. With 1 ♀ indicated to be of class 4 = fL_1l_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	2	2	0
Expected	*2*	*2*	*0*
Mean winter production of ♀ ♀ in indicated class	40.50 eggs	23.00 eggs	

All ♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	7	12	1
Expected	*8*	*10*	*2*
Mean winter production	47.43 eggs	16.25 eggs	0 eggs

While the families in this case are small, the evidence of segregation in about the expected proportions is clear.

B.P.R. ♂ *556.* Indicated constitution = fL_1L_2. fl_1l_2.

This male was hatched in 1908 and used in the breeding pens in 1909. He proved a good breeder and got a fairly large number of adult daughters which were tested in respect to fecundity in the laying year 1909-10. As noted above he was the sire of class 4 ♂ 566. The breeding history of ♂ 556 follows.

Matings: A. With 4 ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	8½	10½	4
Expected	*8.6*	*11.5*	*2.9*
Mean winter egg production of all daughters in indicated class	43.75 eggs	19.60 eggs	0 eggs

V. With 9 ♀ ♀ indicated to be of class 2 = fL_1L_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	10½	10½	0
Expected	*10.5*	*10.5*	*0*
Mean winter egg production of all daughters in indicated class	47.00 eggs	19.60 eggs	

All ♀ Progeny			
Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	19	21	4
Expected	*19.1*	*22*	*2.9*
Mean winter production	46.00 eggs	19.60 eggs	0 eggs

The agreement here between observation and expectation is indeed remarkably close, and with a fairly large progeny.

Summary of results of all matings of class 4 males. Proceeding as before we may bring together here the results for each particular gametic combination taking all individuals together. While class 4 males were not used as often in these experiments as those of class 7, still the numbers involved are sufficiently large to give quite definite evidence regarding the segregation of fecundity factors.

TABLE 17

Showing the results of all matings of class 4 ♂ ♂ × class 1 ♀ ♀
$fL_1L_2 \cdot fl_1l_2 \times fL_1L_2 \cdot Fl_1l_2$

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ progeny
4	17	Observed	21	30	8	59
		Expected	*22.1*	*29.5*	*7.4*	
Mean winter egg production of all ♀ ♀ in indicated class			48.85 eggs	16.34 eggs	0 eggs	

TABLE 18

Showing the results of all matings of class 4 ♂ ♂ × class 2 ♀ ♀
$fL_1L_2 \cdot fl_1l_2 \times fL_1L_2 \cdot FL_1l_2$

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ progeny
3	16	Observed	21	16.5	0	38
		Expected	*19*	*19*	*0*	
Mean winter production of all ♀ ♀ in indicated class.....			50.38 eggs	16.69 eggs		

TABLE 19

Showing the results of all matings of class 4 ♂♂ × class 4 ♀♀
$fL_1L_2 \cdot fl_1l_2 \times fL_1l_2 \cdot FL_1l_2$

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ progeny
2	4	Observed	5	5	0	10
		Expected	*5*	*5*	*0*	
Mean winter production of all ♀♀ in indicated class			43.40 eggs	13.60 eggs		

TABLE 20

Showing the results of all matings of class 4 ♂♂ × all classes of ♀♀
General Summary

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ progeny
4	43	Observed	51½	62½	11	125
		Expected	*51.45*	*62.5*	*11.05*	
Mean winter production of all ♀♀ in indicated class			47.94 eggs	15.34 eggs	0 eggs	

No closer agreement between observation and expectation than is here shown could be expected. The results of the matings discussed in this section confirm completely the general conclusions reached above from an examination of the matings of class 7 males.

Matings of Barred Plymouth Rock males of class 3.

Males of this class have a gametic constitution $fL_1L_2 \cdot fl_1L_2$. That is, they are homozygous with respect to the second, or excess, production factor, and heterozygous with respect to the first. Two males of this type were used in the experiments.

B.P.R. ♂ 65. Indicated constitution = $fL_1L_2 \cdot fl_1L_2$

This male was purchased in 1908 from Mr. Wesley B. Barton, Dalton, Mass. Nothing is known of his breeding so far as

concerns fecundity, but in all probability no particular effort towards breeding for high egg productiveness had ever been made in the stock from which he came. He was bred as a cockerel in the season of 1908 with the results set forth below.

Matings: A. With 1 ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	7	1	1
Expected	6.75	2.25	0
Mean winter production of all ♀ ♀ in indicated class	53.00 eggs	19.00 eggs	0 eggs

B. With 1 ♀ indicated to be of class 6 = fl_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	2	3	0
Expected	2.5	2.5	0
Mean winter production of all ♀ ♀ in indicated class	37.00 eggs	18.67 eggs	

All ♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	9	4	1
Expected	9.25	4.75	0
Mean winter production	49.44 eggs	18.75 eggs	0 eggs

In this case, while the number of successful matings was small, the families were relatively large. In the case of ♀ 366, set down here as probably of class 6, it should be said that this conclusion as to her gametic constitution is reached from a study of her daughters' and granddaughters' behavior. Her own winter egg record was 33, which on this view is regarded as a somatic fluctuation from the L_1 (Under 30) class.

B.P.R. ♂ *68.* Indicated constitution = fL_1L_2. fl_1L_2.

As in the case of ♂ 65 nothing is known regarding the breeding of this bird, it having been purchased from Mr. Geo. W. Hillson, of Amenia, N. Y., early in 1908. It was bred as a cockerel the same season. The only matings to get adult daughters were those with class 1 females. The breeding history is as follows:

Matings: A. With 4 ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

All ♀ Progeny

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	13	5	2
Expected	*15*	*5*	*0*
Mean winter production of all ♀ ♀ in indicated classes	59.00 eggs	25.20 eggs	0 eggs

The facts regarding the two zero birds here are of interest. According to theory no bird of this class should appear from any of these matings. One of these zero birds, E192, laid her first egg March 4, 1909, and proved thereafter, during the reproductive period (March 1 to June 1) to be a fairly good layer, with a total production for the period of 51 eggs.

Her laying during this and the subsequent summer period both in respect to its amount and its distribution, impresses one as like that of a bird carrying L_2 rather than like that of a 'genetic' zero winter layer lacking this factor. I am of the opinion that this was the case. This bird, on such a view, would represent an extreme physiological variant in respect to the beginning of laying. While apparently bearing L_1 this factor did not come to expression until much later than under normal circumstances.

The other zero bird was pathological in respect to her reproductive organs. She never laid an egg and died July 16, 1909. The autopsy record is as follows, plainly showing that the zero record of this bird cannot be taken as any indication whatever of her gametic constitution in respect to fecundity.

Autopsy of E 318, July 16, 1909. Body weight, 1730 grams. Hatched March 31, 1908. Oviduct small: parts of it contained masses of hardened secretion. Ovary with no large oöcytes. One small yolk resorbing. Body cavity filled with masses of hard yolk enclosed in peritoneal sacs. Some of these masses were small and attached to mesentery. Some were large. A large mass filled the dorsal part of body cavity on left side pushing over by a neck and connected by this with a similar mass on right side. This was partly hollow and in the cavity the surface was covered with a fruiting fungus resembling Penicillium. The peritoneum covering the masses of hard yolk formed adhesions with the viscera so that the intestine and oviduct were a bundle of adhesions clinging to these yolk masses.

It is only possible to summarize separately class 3 ♂ matings for class 1 females. This is done in table 21.

TABLE 21

Showing the results of all matings of class 3 ♂ ♂ × class 1 ♀ ♀
fL_1L_2 . fl_1L_2 × fL_1L_2 . Fl_1l_2

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ progeny
2	5	Observed	20	6	3	29
		Expected	*21.75*	*7.25*	*0*	
Mean winter production of all ♀ ♀ in indicated class			56.90 eggs	24.17 eggs	0 eggs	

TABLE 22

Showing the results of all matings of class 3 ♂ ♂ with ♀ ♀ of all classes

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ offspring
2	6	Observed	22	9	3	34
		Expected	*24.25*	*9.75*	*0*	
Mean winter production of all ♀ ♀ in indicated class			55.09 eggs	22.33 eggs	0 eggs	

All matings of class 3 males are summarized in table 22.

The evidence for the segregation of high and low fecundity, as measured by winter egg production is quite as clear from the matings of class 3 ♂ ♂ as from those of class 7 or class 4 ♂ ♂ previously considered.

Matings of Barred Plymouth Rock males of class 2. Four males of this class were used in the experiments. None of them got a large number of adult daughters. It will be noted from table 9 that males of this class (gametic formula fL_1L_2. fL_1l_2) should produce daughters with winter records 'Over 30' and 'Under 30' in equal numbers regardless of the type of females with which the mating is made. The only basis for classifying the females in such matings is then the breeding behavior of their progeny, and particularly their daughters.

B.P.R. ♂ *32.* Indicated constitution = fL_1L_2. fL_1l_2.

This male was hatched from Station stock in the spring of 1907 and bred in 1908. Nothing is known of his ancestry except that his mother was a '200-egg' hen. His breeding history follows:

Matings: A. With 2 ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	4	3	0
Expected	*3.5*	*3.5*	*0*
Mean winter production of all ♀ ♀ in indicated class	52.50 eggs	14.33 eggs	

B.P.R. ♂ *57.* Indicated constituion = fL_1L_2 fL_1l_2.

This male was purchased from Pine Top Poultry Farm, Hartwood, N. Y. in 1908 and bred as a cockerel that year.

Matings: A. With 2 ♀ ♀ indicated to be of class 2 = fL_1L_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	2	1	0
Expected	*1.5*	*1.5*	*0*
Mean winter production of all ♀ ♀ in indicated class	38.00 eggs	24.00 eggs	

B. With 2 ♀ ♀ indicated to be of class 3 = fL_1l_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	4	3	0
Expected	*3.5*	*3.5*	*0*
Mean winter production of all ♀ ♀ in indicated class	62.75 eggs	23.00 eggs	

All ♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	6	4	0
Expected	*5*	*5*	*0*
Mean winter production of all ♀ ♀ in indicated class	54.50 eggs	23.25 eggs	

B.P.R. ♂ *17.* Indicated constitution = fL_1L_2. FL_1l_2.

This cockerel was hatched in 1907 from a '200-egg' mother and was bred in the spring of 1908.

Matings: A. With 2 ♀ ♀ indicated to be of class 3 = fL_1l_2. Fl_1l_2.

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	3	3	0
Expected	*3*	*3*	*0*
Mean winter production of all ♀ ♀ in indicated class	47.00 eggs	12.33 eggs	

B.P.R. ♂ *70.* This cockerel was purchased from Mr. M. L. Chapman, Farmington, Conn., and used in the breeding season of 1908. Nothing is known of his previous history.

Matings: A. With 3 ♀ ♀ indicated to be of class 2 = fL_1L_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	4	5	0
Expected	*4.5*	*4.5*	*0*
Mean winter production of all ♀ ♀ in indicated class	68.25 eggs	19.00 eggs	

B. With 2 ♀ ♀ indicated to be of class 3 = fL_1l_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	2	1	0
Expected	*1.5*	*1.5*	*0*
Mean winter production of all ♀ ♀ in indicated class	51.50 eggs	25.00 eggs	

All ♀ *Progeny.*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	6	6	0
Expected	*6*	*6*	*0*
Mean winter production	62.67 eggs	20.00 eggs	

Summary of results of all matings of class 2 males. The summarized results of the above matings are set forth in table 23.

TABLE 23

Showing the results of all matings of class 2 ♂ ♂ × class 2 ♀ ♀
fL_1L_2 . fL_1l_2 × fL_1L_2 . FL_1l_2

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ progeny
2	5	Observed	6	6	0	12
		Expected	*6*	*6*	*0*	
Mean winter egg production of all ♀ ♀ in indicated class.....			58.17 eggs	19.83 eggs		

TABLE 24

Showing the results of all matings of class 2 ♂ ♂ × class 3 ♀ ♀
fL_1L_2 . fL_1l_2 × fL_1l_2 . Fl_1l_2

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ progeny
3	6	Observed	9	7	0	16
		Expected	*8*	*8*	*0*	
Mean winter production of all ♀ ♀ in indicated class.....			55.00 eggs	18.71 eggs		

TABLE 25

Showing the results of all matings of class 2 ♂ ♂ × all classes of ♀ ♀

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Daughters				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ progeny
4	13	Observed	19	16	0	35
		Expected	*17.5*	*17.5*	*0*	
Mean winter production of all ♀ ♀ in indicated class.....			55.47 eggs	18.31 eggs		

It is clear that the four class 2 males produced a progeny generation, which, though relatively small in absolute numbers, agrees very closely in respect to its gametic distribution with the expected results.

Matings of a Barred Plymouth Rock male of class 8. Males of class 8 are homozygous with respect to the absence of the first production factor, and heterozygous for the second, their gametic formula being fl_1L_2. fl_1l_2. But one bird of this type was used in the experiments.

B.P.R. ♂ 26. Indicated constitution = fl_1L_2 fl_1l_2.

This was one of the original stock in 1908. Nothing further is known of his breeding than that he was the son of a bird that had laid 200 or more eggs in her pullet year. His dam must have been of class 1, since a class 2 ♀ could not produce a class 8 ♂. Male 26 was bred as a cockerel in 1908 with the following results:

Matings: A. With 2 ♀ ♀ indicated to be of class 1 = fL_1L_2 fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	2½	9½	5
Expected	*4.25*	*8.5*	*4.25*
Mean winter production of all ♀ ♀ in indicated class	35.00	9.89 eggs	0 eggs

B. With 5 ♀ ♀ indicated to be of class 4 = fL_1l_2. FL_1l_2.

♀ Progeny

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	6	6	0
Expected	*6*	*6*	*0*
Mean winter productions of all ♀ ♀ in indicated class	69.00 eggs	15.83 eggs	

All ♀ Progeny.

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	8½	15½	5
Expected	*10.25*	*14.5*	*4.25*
Mean winter production	60.50 eggs	12.25 eggs	0 eggs

One of the five females (♀ 397) of class 4 actually laid 31 eggs in her winter period and hence was literally an 'Over 30' bird. There can be no doubt, however, that this record is merely a fluctuation, and that ♀ 397 is really a class 4 bird of the constitution indicated. This is shown by her progeny.

Matings of a Barred Plymouth Rock male of class 1. Males of class 1 are extremely interesting both from the theoretical and the practical standpoint, since they are homozygous with respect to the presence of both fecundity factors. In consequence, *all* the daughters of any male of this class, regardless of the females with which he is mated, should be high producers. In the course of the experiments here under discussion only one male of this type has been used in the breeding pens, and owing to an unfortunate accident he was available for breeding only during a single season. This ♂ no. 550 was a remarkably fine and vigorous bird. He was easily the best bird, in respect to all fancy and utility points, out of the hundreds of cockerels raised the same year. He produced by the mating of a class 3 ♂ (♂ 68, p. 000, supra) and a class 1 ♀. That is,

$$(♂68)\quad fL_1L_2.\ fl_1l_2 \times fL_1L_2\ Fl_1l_2\quad (♀C161)$$
$$\downarrow$$
$$♂550$$
$$fL_1L_2.\ fL_1L_2$$

This is a particularly interesting pedigree to anyone acquainted with the practical breeding and breeders of Barred Plymouth Rocks in this country, because, as already pointed out, ♂ 68 was purchased from Mr. G. W. Hillson, of Amenia, N. Y. Now it is generally supposed, and indeed has been stated by Mr. Hillson in his advertising, that his stock was founded from Mr. E. B. Thompson's 'Ringlet' strain, a stock very well known for quality in color and barring, but not commonly believed to be of any particular value for utility purposes. Yet here we have produced from this strain a male bird of the highest possible utility value, namely one that gets high-producing daughters regularly and without fail, regardless of the females to which he may be mated.

The breeding history of ♂ 550 is as follows:

Matings: A. With 5½ ♀ ♀ indicated to be classes 1 or 2=$fL_1L_2\ Fl_1l_2$ or $fL_1L_2.\ FL_1l_2$.

B. With $4\frac{1}{2}$ ♀ ♀ indicated to be of classes 3, 4, or 6 = fL_1l_2. Fl_1l_2 or fL_1l_2. FL_1l_2 or fl_1L_2. Fl_1l_2.

All ♀ Progeny

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	$16\frac{1}{2}$	$\frac{1}{2}$	1
Expected	*18*	*0*	*0*
Mean winter production of all ♀ ♀ in indicated class	51.25 eggs	1	0 eggs

[1]See p. 312 for explanation of the convention of dividing the birds which lay exactly 30 eggs in the winter period.

The one daughter (F379) with the zero record was evidently abnormal in respect to her reproductive organs. During the last days of September and early October she began and kept up for a period of over a week daily visits to the nest (cf. section on "Matings of Barred Plymouth Rock males with Barred F_1 females") This is *normally* a *sure* indication of approaching laying. Further, birds which begin in this way not only are precocious in laying but make high winter records. This bird, however, stopped at once, and neither visited a nest, nor laid until late the next spring and then laid only a few eggs. There is little doubt that in this case the hereditary basis for high pro luction was present (L_1L_2) but failed of expression for purely physiological reasons. Unfortunately no post-mortem examination of this bird was made, the fact of her abnormality not having been recognized until too late to make such an examination possible.

It was unfortunate that ♂ 550 could not have been used during several breeding seasons. Even with the limited progeny actually available, however, the contrast between this bird and the others which have been discussed above is sufficiently striking.

Doubtful cases. In 1908 a Barred Plymouth Rock ♂ no. 61 was successfully mated with 3 ♀ ♀. The winter production records were as follows:

Mothers' winter production		*Daughters' winter production*		
♀ D157	Under 30	1 over 30	0 under 30	0 zero
♀ D168	Over 30	2 over 30	10 under 30	1 zero
♀ D90	Under 30	2 over 30	5 under 30	0 zero

The case is a difficult one, because of the behavior of certain of the daughters in subsequent matings. The most probable interpretation of the facts is that ♂ 61 belonged to class 4, and that D168 is a ♀ of class 1, but that in certain of her daughters bearing L_2, this character did not come to full expression, giving a winter record of under 30. Three of the 10 daughters of ♀ D168 recorded as 'Under 30' laid 25 or more eggs in the winter period. If we suppose these to be really L_2 birds, we should then have the following *gametic* distribution of 168's daughters.

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	5	7	1
Expected	*4.5*	*6.5*	*2*

This is as close as could be expected.

Female D90 may be of either class 3 or 4. The data at hand do not enable one to determine with certainty between these possibilities. Female D157's only daughter left no adult ♀ offspring, and therefore it is not possible to make any conjecture as to her constitution, beyond the fact that she was probably not of class 1 or 2.

In the case of a number of males the families of adult daughters obtained were so small in size as to make impossible any accurate determination of the gametic constitution of the mothers used. All of these cases are here grouped together in one table.

TABLE 26

Showing the results in respect to fecundity of daughters from pure Barred Rock matings in which the families were too small in size or number to permit classification as to gametic constitution

♂	No. of ♀ ♀ Mated	Daughters' Winter Production		
		Over 30	Under 30	Zero
60	5	6	4	1
16	2	4	1	0
5	2	3	1	0
11	14	14	11	1
527	5	4	4	0
555	8	5	8	0
551	11	9	8	1
Totals.....	47	45	37	3

It will be seen from this table that these families had on the average fewer than two adult daughters each, too small a number with which to work. This makes clear again the difficulty with which one has always to contend in practice in work with fecundity, namely that of getting even reasonably large families of normal *adult* daughters. One hatches a large number of chicks in order to supply thieves, crows, rats, hawks, etc., and finally get a small number of adult females available for the study of fecundity. Fecundity in fowls is not, as has been pointed out before, in all respects an ideal character for the investigation of the laws of inheritance.

Summary of results of all pure Barred Rock matings

The data presented in detail in this section of the paper, which deals with the matings of Barred Plymouth Rock males and females inter se, would appear to demonstrate the following points.

1. That there is a definite and clean-cut segregation (in the Mendelian sense) of high fecundity and low fecundity, the character 'fecundity' being here measured by winter egg production. The mode of inheritance is such as to indicate that winter egg production depends upon two separately inherited physiological factors. The presence of both of these factors (L_1 and L_2) is essential to a *high* fecundity record. The second factor L_2, without which high fecundity never appears is inherited in a sex-correlated manner, such that it is never borne in the same gamete that carries the female sex-factor F.

2. That the things segregated are perfectly definite and distinct. This is shown by the mean or average production records of the birds falling into the several fecundity classes. The birds bearing the factors for high fecundity have mean winter production records ranging from *two to five or six times as great* as the mean production records of birds lacking these high fecundity factors. Such differences as these do not depend upon refined statistical analysis for their detection and appreciation.

While by no means all the possible gametic combinations in respect to fecundity within the Barred Rock breed have yet been made, still the range covered by the data given above is fairly wide. All classes of females except the zero producers (class

5) have been repeatedly tested in the breeding pens in various different combinations. The zero winter producing females have been fairly often bred, but the difficulties of getting chickens hatched within the necessary time limits and in sufficient number to get adult daughters for fecundity work have been too great for the available resources. Of the nine possible types of males six have been tested in various combinations.

It may fairly be said, I think, that in its range, its quality and its amount, the evidence from the pure Barred Rock matings, as set forth in the preceding sections, is sufficient alone to demonstrate the Mendelian inheritance of fecundity in the breed of fowls. If, however, the principles set forth above for Plymouth Rocks are true, they ought to apply, in general at least, to other breeds of fowls and to crosses, with, of course, possible limitations and modifications in particular instances. It is desirable, therefore, to examine the results regarding the inheritance of fecundity in other breeds and crosses. This we may proceed to do.

Cornish Indian Game matings

The strain of Cornish Indian Game fowls used in these experiments is characterized, as has already been pointed out, by very poor egg production. There is no evidence that any of the individuals, either male or female, ever carry the second fecundity factor L_2. These birds therefore represent the extreme condition in the way of low fecundity as compared with the Barred Plymouth Rocks.

The Cornish Indian Game is an old breed and if one may judge from poultrymen's accounts, there certainly have existed in the past, and probably exist now strains of birds belonging to this breed which are fairly good layers. Such strains, which are in marked contrast to the one here used, undoubtedly carry in some combination, the second fecundity factor L_2. There is nothing extraordinary, or contradictory to the results of the present paper, in such a fact (if it be a fact). Indeed it will be shown, in a later section of this paper, how it has been possible experimentally to form synthetically high laying Game hens, i.e., to put the factor L_2 into their hereditary constitution (cf. section on F_2 matings).

Owing to limitation of space and for other reasons it has not been possible to carry on the fecundity studies with this breed on anything like the same scale as with the Barred Rocks. Therefore the numbers here dealt with will be smaller than in the previous section. They will be sufficient, however, to indicate clearly the hereditary constitution of the material. Of the possible types of C.I.G. ♂ ♂ in respect to fecundity as set forth in table 7, two (class 2 and class 3) have actually been used in pure Cornish matings (i.e., C.I.G. ♂ × C.I.G. ♀).

Matings of a Cornish Indian Game male of class 2 (table 7). This ♂, no. 558, was hatched in the spring of 1908 and used to head a pure Cornish pen in 1909. His breeding record indicated that he was of class 2, with a constitution fL_1l_2. fl_1l_2. His breeding history was as follows:

Matings: A. With 5 ♀ ♀ indicated to be of class 1 (Table 8) = fL_1l_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	1	9	0
Expected	*0*	*10*	*0*
Mean winter production of all ♀ ♀ in indicated class	37.00 eggs	8.56 eggs	

B. With 2 ♀ ♀ indicated to be of classes 2 or 3 = fl_1l_2. FL_1l_2 or fL_2l_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	0	5	3
Expected	*0*	*6*	*2*
Mean winter production of all ♀ ♀ in indicated class		8.00 eggs	0 eggs

All ♀ Progeny

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	1	14	3
Expected	*0*	*16*	*2*
Mean winter production	37.00	8.36 eggs	0 eggs

The one bird recorded here as 'Over 30' laid but 37 eggs. Her progeny show clearly and unmistakably that she did not bear L_2. That is to say, her record is a somatic fluctuation above the 30 limit, and has no gametic foundation. The agreement be-

tween observation and expectation on a gametic basis is really perfect for mating A. Taken as a whole the facts speak for themselves. The contrast with the results of Barred Rock matings is striking.

Matings of a Cornish Indian Game male of class 3 (table 7). Male no. 578 was hatched in 1909 and used in the breeding pens the following year. His breeding record shows that he was homozygous with respect to the absence of both fecundity factors, having the constitution fl_1l_2. fl_1l_2. He then belongs to class 3 of table 7. His breeding record is as follows:

Matings: A. With 4 ♀ ♀ indicated to be of classes 2 or 3 = fl_1l_2 . FL_1l_2 or fL_1l_2 Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	1	9	8
Expected	*0*	*9*	*9*
Mean winter production of all ♀ ♀ in indicated classes	39.00 eggs	13.11 eggs	0 eggs

B. With 1 ♀ indicated to be of class 4 = fl_1l_2 Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	0	0	4
Expected	*0*	*0*	*4*
Mean winter egg production of all ♀ ♀ in indicated class			0 eggs

All ♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	1	9	12
Expected	*0*	*9*	*13*
Mean winter production	39.00 eggs	13.11 eggs	0 eggs

Here again as in the previous case the single 'Over 30' record is a somatic fluctuation, without gametic significance. Leaving this out of account, or rather putting it in the 'Under 30' class where it belongs, the agreement between observation and expectation is very close.

Summary of results of Cornish Indian Game matings

Summarizing all pure Cornish matings which involved 2 ♂ ♂ and 20 ♀ ♀ (C.I.G. ♂ × C.I.G. ♀) we have the following results:

All ♀ Progeny.

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	2	23	15
Expected	0	25	15
Mean winter production	38.00 eggs	10.22 eggs	0 eggs

Counting the two 'Over 30' records as somatic fluctuations belonging gametically to the 'Under 30' class the agreement between observation and theory is perfect. This it is seen that the same hypothesis which has been shown to account for the inheritance of fecundity in the Barred Plymouth Rock breed characterized in general by relatively high egg production, also accounts perfectly for the inheritance of this character in the entirely unrelated Cornish Indian Game breed, which is characterized by relatively poor egg production.

Reciprocal crosses of Barred Plymouth Rocks and Cornish Indian Games. F_1 generation

In connection with studies of the inheritance of plumage patterns and colors extensive experiments in crossing these two breeds have been carried out (cf. 40, 41). The results of these experiments in respect to fecundity form a crucial test of the validity of the Mendelian interpretation of the data from pure races set forth in the preceding pages. If the interpretation which has been given is correct it should account for the observed results in the F_1, F_2 and subsequent cross-bred generations. Should it fail when subjected to this test, it would necessitate its acceptance with great reservation, if at all, for the pure races. On the other hand, agreement of the results from these cross-bred matings with those obtained from the pure-bred would afford the strongest confirmation which it is possible experimentally to obtain of the essential soundness of the general conclusions reached.

Matings of Barred Plymouth Rock males and Cornish Indian Game females. Two different males were used successfully[13] in matings of this sort. Both of these birds were of class 7, having the gametic constitution fl_1L_2. fl_1L_2. One of them (♂ 554) was used in a number of pure B.P.R. matings with results already discussed in a previous section.

Matings of B. P. R. ♂ 559. Indicated constitution = fl_1L_2. fl_1L_2.

Matings: A. With 9 Cornish ♀ ♀ indicated to be of classes 2 or 3 = fl_1l_2. FL_1l_2 or fL_1l_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	18	17	2
Expected	*18.5*	*18.5*	*0*
Mean winter egg production of all ♀ ♀ of indicated class ...	46.38 eggs	15.00 eggs	0 eggs

If we suppose the two zero birds to represent somatic fluctuations the agreement between observation and expectation is very close. Both these zero birds were late hatched and all the facts regarding them indicate that they carried L_2, but for physiological reasons did not bring it to expression.

B. With 1 Cornish ♀ indicated to be of class 1 = fL_1l_2 . FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	5	1	0
Expected	*6*	*0*	*0*
Mean winter egg production of all ♀ ♀ of indicated class	42.75 eggs	20 eggs	

There is little doubt about this mating being of the type indicated, in spite of the one bird laying 'Under 30.' Her winter record was 20 eggs and she was a late (June) hatched bird. She probably carried L_2, but this cannot be positively asserted because no male bird from her was mated. Only in this way could the point be settled.

[13] i.e., got adult daughters.

All ♀ Progeny

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	23	18	2
Expected	*24.5*	*18.5*	*0*
Mean winter production	46.09 eggs	15.22 eggs	0 eggs

Matings of B.P.R. ♂ 554. This male has been shown above from his mating with Barred Rock females, to be of class 7 with the gametic constitution flL_2. flI_2. He was successfully mated with one Cornish Indian Game ♀ of class 2. From this mating we have

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	1	3	0
Expected	*2*	*2*	*0*
Mean winter production	49	19.33 eggs	0 eggs

Putting all the results together we have for *all matings of B.P.R. ♂ ♂ × C.I.G. ♀ ♀*

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	24	21	2
Expected	*26.5*	*20.5*	*0*
Mean winter production	46.22 eggs	15.86 eggs	0 eggs

We see here the same agreement between observation and expectation which has appeared in the previous cases with pure matings.

Attention may next be turned to the reciprocal cross.

Matings of Cornish Indian Game males and Barred Plymouth Rock females. Four different Cornish males were used in these matings and got adult daughters. Their breeding histories follow.

Matings of C.I.G. ♂ 558. This bird was used in pure Cornish matings and there shown to be of class 2 (C.I.G.) with constitution fL_1l_2. flI_2. His breeding history in producing F_1 females was as follows:

Matings: A. With 2 B. P. R. ♀ ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	4	14	2
Expected	0	15	5
Mean winter production of all ♀ ♀ in indicated class	51.75 eggs	15.79 eggs	0 eggs

The four birds with 'Over 30' records are apparently outstanding exceptions. It should be noted that these birds came from mothers whose gametic constitution was of the general type L_1. L_2. This would seem to suggest that in this case the presence of L_2 in the mother, even though it did not pass to tny of the F-bearing gametes, nevertheless in some manner or other modified the L_1 in these gametes so that a higher production in the progeny resulted. In other words. these cases suggest 'intra-zygotic influence' of the gametic factors upon one another, such as is frequently suggested by the conditions observed in heterozygotes, and lately has been discussed by Davenport (6, 7) and Laughlin (23). The winter records of these four birds are to be regarded as wide fluctuations, since when bred they gave no indications of carrying F_2.

B. With 1 B. P. R. ♀ indicated to be of class 3 = fL_1l_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	0	3	1
Expected	0	3	1
Mean winter production of ♀ ♀ in indicated class		6.00 eggs	0 eggs

All ♀ *Progeny.*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	4	17	3
Expected	0	18	6
Mean winter production	51.75 eggs	14.06 eggs	0 eggs

Matings of C.I.G. ♂ 557. Indicated constitution: class 3 (C.I.G.) ♂ = fl_1l_2. fl_1l_2.

Matings: A. With 6 B.P.R. ♀ ♀ indicated to be of class 2 = fL_1L_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	0	17	0
Expected	*0*	*17*	*0*
Mean winter production of ♀ ♀ in indicated class		12.88 eggs	

B. With 1 B.P.R. ♀ indicated to be of class 4 = fL_1l_2. FL_1l_2.

♀ Progeny

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	0	1	0
Expected	*0*	*1*	*0*
Observed winter production		10 eggs	

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	0	18	0
Expected	*0*	*18*	*0*
Mean winter production		12.72 eggs	

The accordance between observations and expectation here is perfect.

Mating of C.I.G. ♂ 529. Indicated constitution: class 2 (C.I.G. ♂) = fL_1l_2. fl_1l_2.

Matings: A. With 1 ♀ indicated to be of class 1 = fL_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	1	1	1
Expected	*0*	*2.25*	*0.75*
Observed winter production	46 eggs	13 eggs	0 eggs

This mating by itself is, of course, without any particular significance.

B. With 6 ♀ ♀ indicated to be of class 2 = fL_1L_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	5	12	0
Expected	*0*	*17*	*0*
Mean winter productions of all ♀ ♀ in indicated class	41.60 eggs	11.67 eggs	

Here, again, as in the case of ♂ 558 there are seen to be several birds with winter records of over 30 eggs, when none is expected.

C. With 3 ♀ ♀ indicated to be of class 7 = fl_1L_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	1	3	2
Expected	*0*	*3*	*3*
Mean winter production of all ♀ ♀ in indicated class	45 eggs	13.00 eggs	0 eggs

All ♀ Progeny.

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	7	16	3
Expected	*0*	*22.25*	*3.75*
Mean winter production	42.71 eggs	12.00 eggs	0 eggs

The seven birds with records 'Over 30' belong gametically to the 'Under 30' class, and their records are somatic fluctuations. This is shown both by their history and by their behavior in F_2, all having been bred.

Matings of C.I.G. ♂ 578. This male has been shown from his matings with pure Cornish females to belong to class 3 of C.I.G. ♂ ♂ (= fhl_2. fhl_2). His matings with Barred Rock females are as follows:

Matings: A. With 2 B.P.R. ♀ ♀ indicated to be of class 2 = fL_1L_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	0	3	0
Expected	*0*	*3*	*0*
Mean winter production of daughters		6.33 eggs	

B. With 1 ♀ indicated to be of class 4 = fL_1l_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	1	4	0
Expected	*0*	*5*	*0*
Mean winter production of daughters in indicated class	42 eggs	11.00 eggs	0 eggs

All ♀ Progeny.

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	1	7	0
Expected	0	8	0
Mean winter production	42 eggs	9.00 eggs	

There are no data from which to make sure whether the one bird with an 'Over 30' record represented a fluctuation from the 'Under 30' class. It probably did, but this cannot be positively asserted.

Summary of all F_1 matings

Putting together the results of the matings of all Cornish Indian Game males with Barred Rock females, we have for the actual observations:

♀ *Progeny—Raw Data*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	12	58	6
Expected	0	66.25	9.75
Mean winter production	45.67 eggs	12.46 eggs	0 eggs

In view of the fact that the 11 of the 12 birds with 'Over 30' records represent somatic fluctuations from the 'Under 30' class it is desirable to present another summary table in which the progeny are distributed in accordance with their gametic constitution.

♀ *Progeny on Gametic Basis*

Winter Production:	*Over 30* (L_1L_2)	*Under 30* (L_1l_2)	*Zero* (l_1l_2)
Observed	1	69	6
Expected	0	66.25	9.75

The contrast between these distributions and those of the reciprocal cross discussed before is very striking. Taken together these reciprocal crosses support strongly the general hypothesis of fecundity inheritance here being tested.

Matings of the second cross-bred (F_2) generation

The F_1 birds discussed in the preceding sections were mated in all possible ways *inter se* and with the parent forms. The results of these matings will be discussed in the present section.

At the outstart it should be noted that in spite of the fact that as many F_2 birds were hatched and reared as the available facilities would permit, nevertheless, the number of adult daughters available for fecundity study is small in case of some of the matings. There are several reasons for this. Besides the obvious one such as mortality, depredations of thieves, hawks, crows, rats and the like, there is another important but not so obvious one. This is the failure or great difficulty experienced in getting certain of the F_2 cross breds to grow into normal, full-sized, healthy adult birds. After rather wide experience in handling cross-bred chicks, I am convinced that certain gametic combinations which are to be expected on Mendelian theory, and can be produced in the expected numbers in the breeding pen, are nevertheless physiologically abnormal or unsound. Such birds do not make a normal growth, but in spite of the best care and attention grow up into stunted weaklings, which always show, both in their structure and their physiological economy, the effect of this retarded, abnormal development. I am further convinced that this result is primarily due to the hereditary constitution of the individuals in question. Certain combinations of hereditary factors do not produce physiological sound and vigorous zygotes.

Of course, there is nothing novel in such a result. It is of a piece, for example, with the parts respecting the relation between hereditary constitution and physiological vigor in maize, which have been so clearly set forth and analyzed by Shull (45, 46, 47) and East (9). Other examples of the same phenomenon might be cited. The whole phenomenon is precisely what would be expected from Johannsen's general conception of inheritance and ontogeny (22).

This relationship between hereditary constitution and physiological constitution or normality takes on particular significance when one is dealing with fecundity. As has been pointed out earlier in this paper one cannot expect to get a normal somatic expression of the hereditary constitution in respect to fecundity unless the bird is a physiologically normal, well-developed individual. Stunted, under-developed, or physiologically unsound birds will lay but very few if any eggs, regardless of what fecundity factors it may carry. A marked difference is here apparent between structural and physiological characters so far as

the study of inheritance is concerned. A definite structure either is or is not present in the zygote, however weak physiologically the individual may be. But if the general capability of an organism with respect to the transformation of matter and energy is markedly reduced, then all physiological characters will be affected, and fail to reach complete normal expression.

In the study of cross-bred poultry I have found pure extracted whites from crosses involving originally two heavily pigmented parent races to be conspicuously good examples of the phenomenon under discussion. It is only very exceptionally, in my experience, that such white birds are physiologically normal. Indeed because of this fact it is only with the greatest difficulty, and after many failures, that I have been able to get such extracted whites to breed, and thus form a pure white race. If the hens lay eggs, which some do not do, they are usually either infertile, or else all the embryos die at an early stage. These facts have some bearing on the popular belief of animal breeders that whites in general are delicate in constitution and hard to rear. This belief is so well known that it is not necessary to cite in detail references regarding it in the literature.

As a consequence of the above considerations, I have felt justified in leaving out of account, or rather in considering apart from the others, a few of the F_2 individuals, in all some 7 out of over 200 F_2 birds all told. In each case these birds were physiologically abnormal, and obviously so to the most casual observer. The fact that they did not lay was no criterion whatsoever of their hereditary constitution. In order that there might be no possibility of unfairly influencing ratios by leaving these birds out, the whole families (usually of two or three individuals only) to which they belonged have been rejected. As a matter of fact whenever one individual in a family is physiologically abnormal in this way all the other members will usually show the same condition in greater or less degrees.

In the F_2 generation following the reciprocal crossing of Barred Rocks and Cornish Indian Games there are a number of possible matings. The nature of these matings and the results as to color and pattern have been discussed in another place (41). That paper may be referred to in case one is not clear as

to the nature of the matings. The different matings will be discussed in the following order.

1. F_1 ♂ (out of B.P.R. ♂ × C.I.G. ♀) × F_1 ♀ ♀, barred and non-barred.

2. F_1 ♂ (out of C.I.G. ♂ × B.P.R. ♀) × F_1 ♀ ♀, barred and non-barred.

3. F_1 ♂ (out of B.P.R. ♂ × C.I.G. ♀) × B.P.R. ♀ ♀

4. F ♂ (out of B.P.R. ♂ × C.I.G. ♀) × C.I.G. ♀ ♀

5. F_1 ♂ (out of C.I.G. ♂ × B.P.R ♀) × B.P.R. ♀ ♀

6. F_1 ♂ (out of C.I.G. ♂ × B.P.R. ♀) × C.I.G. ♀ ♀

7. B.P.R. ♂ ♂ × F_1 Barred ♀ ♀

8. B.P.R. ♂ ♂ × F_1 non-barred ♀ ♀

9. C.I.G. ♂ × F_1 ♀ ♀ Barred and non-barred

It will be recalled that the *barred* F_1 females come from the mating B.P.R. ♂ × C.I.G. ♀, and that the *non-barred* (*black*) F_1 females comes from the reciprocal mating C.I.G. ♂ × B.P.R. ♀.

Matings of F_1 ♂ 576 with F_1 females. The pedigree of F_1 ♂ 576 was as follows:

B.P.R. ♂ 559 (flL_2. flL_2) × C.I.G. ♀ 456 (fL_1l_2. Fll_2)

↓

F_1 ♂ 576

The hereditary constitutions of both ♂ 559 and ♀ 456 were known, both from their pedigrees and their progeny in other matings. From this pedigree it is evident that the gametic formula for ♂ 576 must be either flL_2. fL_1l_2 or $fl_1L_2fll_2$. A study of his progeny in all matings shows clearly that it is actually the former. In other words he produced gametes of four kinds, viz., flL_2, fL_1L_2, fL_1l_2, fll_2.

This bird was mated with barred F_1 ♀ ♀ which had been produced by the following mating.

B.P.R. ♂ 559 (*flL*₂. *flL*₂) × C.I.G. ♀ ♀ of type *fLl*₂. *Fll*₂

↓

A. *flL*₂. *FLl*₂-Winter record over 30

and

B. *flL*₂. *Fll*₂-Winter record under 30

Male 576 was mated only with ♀ ♀ of the A class,[14] namely those having a gametic constitution *flL*₂. *FLl*₂, and producing two sorts of *F*-bearing gametes, *Fll*₂ and *FLl*₂.

This same ♂ 576 was mated with non-barred (black) F_1 females which had been produced in the following way.

C.I.G. ♂ 558 or 529 (*fLl*₂. *fll*₂) × B.P.R. ♀ ♀ some of which were of type *fLL*₂. *Fll*₂, and some *fll*₂. *FLl*₂ (both producing *F*-bearing gametes of two kinds *FLl*₂ and *Fll*₂.

↓

A. *fLl*₂. *FLl*₂, Winter record under 30
B. *fll*₂. *FLl*₂, Winter record under 30
C. *fLl*₂. *Fll*₂, Winter record under 30
D. *fll*₂ *Fll*₂, Winter record zero.

The three non-barred ♀ ♀ with which ♂ 576 was bred were of the B-C type, producing two kinds of *F*-bearing gametes, *FLl*₂ and *Fll*₂. They were thus identical, so far as concerns *F*-bearing gametes with the barred F_1 birds with which ♂ 576 was mated. All the progeny may then be treated together since all did, as a matter of fact, lead to the same result, having regard to the errors of sampling in such statistically small lots.

[14] It would of course be desirable to have data from the other mating, ♂ 576 × B ♀ ♀. If one could have foreseen what the mechanism of the inheritance of fecundity was going to turn out to be, such matings would have been made. Actually these cross bred birds were being studied primarily with reference to color characters, and the matings were made relative to that line of investigation. Naturally highly fecund females would be chosen as breeders whenever possible, in order to get more chickens for the color studies. Actually, however, all of the possible gametic combinations in respect to fecundity were tested in F_2 either from one mating or another.

TABLE 27

Showing the results of mating F_1 ♂ 576 with F_1 ♀ ♀
Type of mating: fl_1L_2 . fL_1l_2 × fl_1L_2 . FL_1l_2 and (or) *fL_1l_2 . Fl_1l_2*

Individuals Used in These Matings		Winter Record of Daughters			
♂	♀	Over 30	Under 30	Zero	Total adult ♀ progeny
576	F68	4	2	0	6
576	F89	0	3	0	3
576	F41	1	3	0	4
576	F79	1	3	1	5
576	F416	0	0	2[1]	2
576	F421	0	2	2	4
576	F33	5	3	2	10
576	F415	0	4	1	5
Total observed		11	20	8	39
Total Expected		14.6	19.5	4.9	
Mean winter production of ♀ ♀ in indicated class		42.81 eggs	12.05 eggs	0 eggs	

[1] These two individuals ought really to be excluded on the ground of physiological abnormality of the sort discussed at the beginning of this section. Neither of them made a normal growth. No poultrymen would have regarded these birds as reliable material for the study of egg production. Leaving these two birds out the totals stand as follows:

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	11	20	6
Expected	*13.9*	*18.5*	*4.6*

The same kind of evidence for the segregation of different degrees of fecundity which has been seen in all the previous matings appears again in these F_2 birds.

Matings of F_1 ♂ 577 with F_1 females. This F_1 ♂ 577 was produced in the following way:

C.I.G. ♂ 558 (fL_1l_2. fl_1l_2) × B.P.R. ♀ 234 (fL_1l_2. Fl_1l_2)

↓

F_1 ♂ 577

Such a mating as this would be expected to produce males of four (really three *different*) kinds as follows:

A. fL_1l_2. fL_1L_2 C. fl_1l_2. fL_1L_2
B. fL_1l_2. fl_1L_2 D. fl_1l_2. fl_1L_2

The results indicate that ♂ 577 was of the last (D) type, producing two kinds of gametes, fl_1l_2 and fl_1L_2. He was mated with 4 barred F_1 ♀ ♀ and 4 black F_1 ♀ ♀. All of these females, as in the preceding case, produced F-bearing gametes of

two kinds in equal numbers; $Fl:l_2$ and FL_2l_2. Of these matings three produced small families in which all of the individuals were so far from being normal physiologically that they cannot fairly be included in the tabulation. The details regarding them are as follows. From one barred F_1 ♀ was produced two adult daughters, both of which were undersized and stunted in development, and failed to lay. One of these daughters died early in the year. From one of the matings with black F_1 ♀ ♀ only one adult daughter was obtained, which again failed to develop normally and was only put into the adult house because of its interest from the standpoint of color inheritance. Another of the matings with a black F_1 ♀ produced four adult daughters. Two of these were extracted whites and very small, poor specimens. The whole family was saved because of these birds. Neither of them laid. Of the other sisters one died early in the laying year, never having laid. It, like the other members of the family, was from the start a weakling. Finally the fourth sister made a winter record of 8 eggs. It presented the same evidence of abnormality as the other sisters, and its egg record could by no means be taken as a just indication of its gametic constitution in respect to fecundity. No one of the seven birds under discussion would ever by any chance whatever have been put in the laying house as normal individuals for the study of fecundity. The only reason they ever were put in was simply, as already explained, because the primary object of the F_2 birds as a whole was the study of color and pattern inheritance. Even though a bird is an undeveloped weakling physiologically one may make a record of its plumage color and pattern, and see whether these change with advancing age. However, since these birds really were in the adult house, and in order to forestall the possibility of a suggestion that any records were suppresed in this study of fecundity, it has seemed advisable to take the space for the above detailed discussion of the matter.

The records for the other matings of F_1 ♂ 577 are given in table 28.

Matings of F_1 576 with Barred Plymouth Rock females. This F_1 ♂ was mated with three pure Barred Rock ♀ ♀ of class 2 (table 6). The results of these matings are shown in table 29.

TABLE 28

Showing the results of mating F_1 ♂ 577 with F_1 ♀ ♀
Type of mating: fl_1l_2 . $fl_1L_2 \times fl_1L_2$. FL_1l_2 and fL_1l_2 . Fl_1l_2
Gametes: fl_1l_2 and fl_1L_2. F-bearing gametes: FL_1l_2 and Fl_1l_2

Individuals Used in These Matings		Winter Record of Daughters			
♂	♀	Over 30	Under 30	Zero	Total adult ♀ progeny
577	F401	0	3	0	3
577	F18	0	2	1	3
577	F44	2	4	1	7
577	F99	2	2	0	4
577	F418	1	5	5	11
Total observed		5	16	7	28
Total Expected		*7*	*14*	*7*	
Mean winter production of ♀ ♀ in indicated class		36.33 eggs	11.25 eggs	0 eggs	

TABLE 29

Showing the results of mating F_1 ♂ 576 with Barred Rock ♀ ♀
Type of mating: fl_1L_2 . $fL_1l_2 \times fL_1L_2$. FL_1l_2

Individuals Used in These Matings		Winter Record of Daughters			
♂	♀	Over 30	Under 30	Zero	Total adult ♀ progeny
576	1107	1	1	0	2
576	F115	1	2	0	3
576	F111	7½	3½	0	11
Total observed		9½	6½	0	16
Total Expected		*8*	*8*	*0*	
Mean winter production of ♀ ♀ in indicated class		46.78 eggs	22.83 eggs		

These results are suggestive in connection with the problem of the absolute fecundity value of the same genes from different sources, a matter which will be fully discussed later. The figures give clear evidence of Mendelian segregation of high and low fecundity.

Matings of F_1 ♂ 576 with Cornish Indian Game females. There were but two matings of ♂ 576 with pure Cornish Indian Game ♀ ♀ which produced adult female offsprings. Other matings were made but got no adult progeny. The successful

matings were with C.I.G. ♀ ♀ of constitution *flₗlₗ. FlₗlₗL*. The results were as follows:

♂ 576 fl_1L_2. fL_1l_2 × fl_1l_2. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	0	3	1
	0	2	0
Total observed	0	5	1
Total expected	*1.5*	*3*	*1.5*
Mean winter production of ♀ ♀ in indicated class		11.80 eggs	0 eggs

The numbers here are too small to give definite results, but there is nothing incompatible in the observations, having regard to the smallness of the numbers, with what would be expected.

Matings of ♂ F₁ 557 with Barred Plymouth Rock females. There were three matings of this sort, but the families were all small. The females used were of class 2 (table 6). The results were as follows:

♂ 577 fl_1l_2. flL_2 × fL_1L_2. FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
(♀ 1118)	0	1	0
(♀ F350)	1½	1½	0
(♀ F235)	1	2	0
Total observed	2½	4½	0
Total expected	*3.5*	*3.5*	*0*
Mean winter production of ♀ ♀ in indicated class		35.00 eggs	11.25 eggs

Again the numbers involved are too small to be of any particular significance when taken by themselves. They are in conformity, however, with all the other data and therefore have cumulative value.

Matings of F₁ ♂ 577 with Cornish Indian Game females. Two matings only of this sort got adult female progeny. The

families are small. The pure Cornish females used were of constitution fL_1l_2. Fl_1l_2 The results follow.

δ 577 fl_1l_2. $fl_1L_2 \times fL_1l_2$. Fl_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
(♀ F7)	0	1	1
(♀ F11)	0	2	1
Total observed	0	3	2
Total expected	*1.25*	*2.5*	*1.25*
Mean winter production of ♀ ♀ in indicated class		7.33 eggs	0 eggs

Matings of Barred Plymouth Rock males with Barred F_1 females. While several matings were made here they all fell into one or the other of two gametic types. The Barred Rock males males used in these matings have, of course, already had their gametic constitutions determined through their matings with pure Barred Rock females.

A. Type of mating: fl_1L_2. $fl_1L_2 \times fl_1L_2$. FL_1l_2. The results of this type of mating are shown in table 30.

There are several points which need to be noted about this table. While in general it is apparent that the observed result falls out in fair accord with expectation, the three zero birds are outstanding exceptions. No zero birds should occur in any of these matings. A careful study of the individual cases, however, indicates that only one of these apparent exceptions is really such. Two of these zero birds were very late hatched and began laying immediately after March 1, i.e., just after the arbitrary point of ending the winter period. Their records during the spring period were such as to indicate that they bore the factor L_1, and not that they lacked it. The third zero bird (no. 558) was an extremely interesting case. Something was at fault physiologically with her reproductive organs, as a result of which she never laid an egg. However, she gave clear evidence that she bore the factor L_1 (or L_2—not both) gametically. This she did through her nesting records. For some years past records have been kept in this work not only of when a hen

TABLE 30

Showing the results of mating class 2 B.P.R. ♂ ♂ with high laying Barred F_1 ♀ ♀

Mating		Observed Winter Production of Daughters		
B. P. R. ♂	Barred F_1 ♀	Over 30	Under 30	Zero
552	424	3	5	0
554	87	0	4	0
563	412	7	1	0
564	405	7	2	0
567	425	2	1	3
562	404	½	½	0
Total observed		19½	13½	3
Total Expected		*18*	*18*	*0*
Mean winter production		57.16 eggs	12.69 eggs	

visited a nest and laid, but also when she visited a nest and did not lay. A large number of records have been accumulated of birds which go through the whole process of nesting and laying except that they do not discharge any eggs from the body. It was hoped to publish a paper on this subject, which throws light on the problem of the physiology of egg production, before the present paper appeared. This has not been possible owing to pressure of other work, so it will be necessary to take a little space here to discuss certain phases of this subject. It has been shown experimentally in the laboratory that if the oviduct of a normal healthy hen, with a normal ovary, is ligated, transected or removed entirely, without injury to the ovary, such a bird goes regularly through the entire process of laying, save for the extrusion of an egg, which is physically impossible. The '*n*' (nesting) record of such a bird is precisely like a normal egg record, showing the same phenomena of rhythm and cycles. Each day's '*n*' in the record of such a bird represents an egg[15] which she would have laid, had she been physically capable of so doing.

Birds in which the oviduct is occluded through some diseased condition often behave in this manner. It may result from other abnormal conditions also. With this explanation, the following

[15] Of course this does not mean that when a bird visits a nest twice in the same day she would have laid two eggs that day had she been normal. Many laying birds have the habit of visiting the nest once or twice in the same day before actually laying.

record of ♀ 558, will be clear, it being understood that '*n*' denotes a visit to a nest and the performance of those acts characteristically associated with the laying of an egg, but without the extrusion of an actual egg.

From this record taken in connection with other similar cases studied in his laboratory, there can be no doubt that ♀ 558 belongs gametically in the class 'Under 30.'

Another point is with reference to the mating ♂ 564 × ♀ 405. The excess of 'Over 30' birds here is in part due to the fact that two birds, which have winter records respectively of 32 and 34 eggs and are almost certainly to be regarded as somatic fluctuations above the division point at 30 are included in the 'Over 30' class.

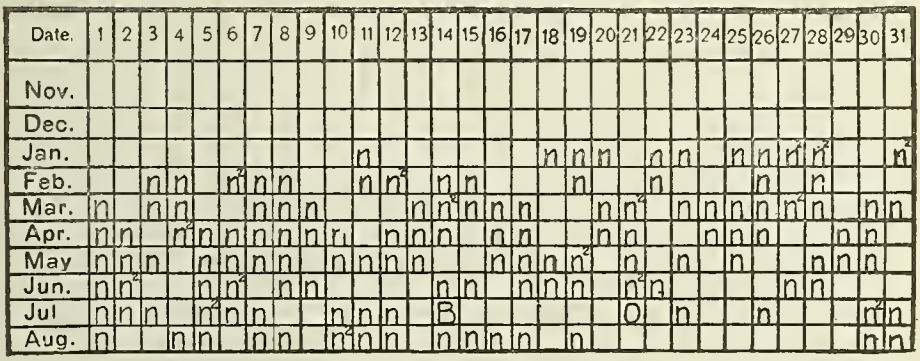

Fig. 452. Nesting record of ♀ 558. '*n*' denotes a visit to the trap-nest. n^2 indicates that the bird visited the nest twice on the same day. *B* indicates that the bird became broody, and *O* that she ceased manifestations of broodiness.

If the totals are modified in accordance with the above suggestion we get

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed: (modified)	$17\frac{1}{2}$	$17\frac{1}{2}$	1
Expected	*18*	*18*	*0*
Mean winter production	60.00 eggs	15.40 eggs	0 eggs

B. Type of mating: $fL_1L_2.\ fl_1l_2$ or $fL_1l_2.\ fl_1L_2$ } × $fl_1L_2.\ FL_1l_2$

♀ *Progeny*

Mating		Observed Winter Production of Daughters		
B. P. R. ♂	Barred F1 ♀	Over 30	Under 30	Zero
566	419	2	3	1
Expected		*2.25*	*3*	*0.75*
Mean winter production		46.50 eggs	13.67 eggs	0 eggs

While this single family is small the three classes expected are represented and in as near the right proportion as could be expected.

Putting together all the results for B.P.R. ♂ ♂ × Barred F_1 ♀ ♀ we get:

♀ *Progeny*

Unmodified Data

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	21½	16½	4
Expected	*20.25*	*21*	*0.75*

Data modified in accordance with physiological facts regarding individual birds

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	19½	20½	2
Expected	*20.25*	*21*	*0.75*

Matings of Barred Plymouth Rock males and F_1 Black females. A number of matings of this type were made, representing several different gametic combinations. The following B.P.R. males were used in these matings. The class and gametic constitution given are those which have been brought out by the pure B.P.R. matings.

Bird No.	Class (Table 5)	Gametic Constitution
552, 554, 562, 573, 564, 567	1, 1, 1, 1, 1, 1	$fhL_2 \cdot fhL_2$
569	4	$fL_1L_2 \cdot fhl_2$

Of these males four, namely 552, 554, 573 and 564, were mated with females whose sire was C.I.G. ♂ 557. These birds

all had the gametic constitution fhl_2. FL_1l_2, as shown in the section on the F_1 birds. The results of these matings are shown in table 31.

The observed figures are a rather bad, though not an impossible, approximation to the expected Mendelian half. The means indicate, however, that there is a definite segregation of the two classes. It is possible that the discrepancy in the ratio finds its explanation in a difference in the potency or absolute fecundity value of the Cornish Indian Game L_1 factor and the same factor in the Barred Plymouth Rock.

TABLE 31

Showing the results of matings of the type B.R.P. ♂ fl_1L_2 . fl_1L_2 × *Black* F_1 ♀ fl_1l_2 . FL_1l_2

Number of Individuals Involved in Matings of This Type		Winter Egg Production of Daughters F_2				
♂♂	♀♀	Class	Over 30	Under 30	Zero	Total adult ♀ progeny
4	4	Observed	5	14	0	19
		Expected	*9.5*	*9.5*	*0*	
Mean winter egg production of all ♀ ♀ in indicated class.....			37.00 eggs	11.14 eggs		

Two of the class 7 B.P.R. males (562 and 567) were mated with two F_1 blacks whose sire was C.I.G. ♂ 558. It has already been shown from the pure Cornish and F_1 matings that this Cornish ♂ 558 had the gametic constitution fL_1l_2. fhl_2. In respect to fecundity his F_1 daughters in the 'Under 30' class were gametically of two types: viz., fL_1l_2. Fhl_2 and fL_1l_2. FL_1l_2. None of the second type were used in these matings. Only a small progeny resulted from the mating of the two females of the first type. The actual results were as follows:

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	2	4	0
Expected	*3*	*3*	*0*
Mean winter egg production of all ♀ ♀ in indicated class ..	38.00 eggs	8.5 eggs	

B.P.R. ♂ 569 was mated with a black F_1 ♀ sired by C.I.G. ♂ 529. Only two daughters were obtained. Both made winter records under 30 eggs. The number of daughters is too small ot have any significance, or to make classification possible.

Putting all the results together (with the exception of the two individuals just noted as not capable of classification) we have:

F_1 ♀ Progeny from matings of B.P.R. ♂ ♂ × Black F_1 ♀ ♀

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	7	18	0
Expected	*12.5*	*12.5*	*0*
Mean winter production	37.29 eggs	10.55 eggs	

There is clear evidence of segregation here but there is a defect in the observed numbers in the 'Over 30' class. After careful study of all the facts a possible explanation of this appears to me that the absolute degree of fecundity manifested somatically when L_1 is present in the gametes may be less if the L_1 comes from a Cornish Indian Game than if it comes from a Barred Plymouth Rock. In other words it appears to be the case that what may be called the absolute fecundity value or worth of L_1 is different in these two breeds. An indication that this is the case is found in the following figures. In the case of pure C.I.G. matings the factor L_2 is not present. All females in the 'Under 30' class are therefore either L_1h or L_1L_1 in type. The mean winter production of all pure C.I.G. ♀ ♀ in the 'Under 30' class is 10.22 eggs. The mean winter production of all pure B.P.R. ♀ ♀ in the 'Under 30' class is 15.61 eggs. The probable errors in both cases are less than 1. Of course the 'Under 30' class in the case of B.P.R. ♀ ♀ includes the following gametic types: L_1h, L_1L_1, hh, and L_2h. The last two do not occur in the pure C.I.G.'s. Granting the greatest conceivable influence to this, it is still evident that the L_1 factor of a Barred Rock probably means a higher winter production than the L_1 of a Cornish Game. But if this is true then plainly the division or upper limiting point for the low fecundity class should not be at 30 eggs but at some lower point in the case of females bearing L_1 from a Cornish Indian Game source. If it be kept at 30 eggs for all birds, and there is a difference in the absolute fecundity value of the factors, then plainly some birds will be put in the

low fecundity class, because of an 'Under 30' record, although they really carry L_2 and belong in the high fecundity class. Such a state of affairs would account for just such discrepancies as those observed in the matings under discussion.

Matings of Cornish Indian Game males with Black and Barred F_1 females. Only one C.I.G. male was used in these F_2 back-cross matings. This was C.I.G. ♂ 578. As will presently appear, it is to be regretted that other Game males were not used, because of certain peculiarities arising in the results of some of these matings. From pure Cornish and F_1 matings ♂ 578 has been shown to have the gametic constitution fl_1l_2. fl_1l_2.

Male 578 was mated with 3 black F_1 females indicated to be of the type fL_1l_2 FL_1l_2, with the following results:

Matings: C.I.G. ♂ $f\ l_1l_2$ $f\ l_1l_2$ × F_1 ♀ fL_1l_2 FL_1l_2.

♀ *Progeny*

Winter Production:	*Over 30*	*Under 30*	*Zero*
Observed	1	9	1
Expected	*0*	*11*	*0*
Mean winter production	41 eggs	9.67 eggs	0 eggs

It will be noted that the one 'Over 30' bird laid but 41 eggs. The record probably represents a fluctuation from the 'Under 30' class. In general the agreement between observation and expectation is satisfactory.

Turning to the matings of ♂ 678 with barred F_1 females we meet the only case in the whole investigation which is apparently unconformable. It will therefore be well to discuss it in detail. The facts are these: ♂ 578 was mated with four barred F_1 females, of which three were in the 'Over 30' class and one was a poor layer. When mated with any of these three high laying birds one half of 578's daughters should have been in the 'Over 30' and one-half in the 'Under 30' class. Mated with the poor layer only zero birds should have resulted. Nothing like this actually happened. The observed outcome was that shown in the following table:

Mating 699 (♂578 × ♀411) gave 13 adult daughters, with winter records as follows: 62, 60, 56, 32, | 30, | 28, 27, 26, 26, 7, 5, 5, 2.

Mating 700 (♂578 × ♀422) gave 7 adult daughters with winter records as follows: 47, 47, 33, | 26, 19, 15, 9.

Mating 701 (♂578 × ♀414) gave 5 adult daughters with winter records as follows: | 23, 16, 5, 0, 0.

Mating 702 (♂ 578 × ♀ 423) gave 11 adult daughters with winter records as follows: 40, 34, | 28, 26, 21, 20, 20, 17, 15, 13, 10, 4.

These records are characterized by four striking facts: (*a*) the large number of 'Over 30' records when none is expected, (*b*) the large number of high 'Under 30' records, (*c*) the absence except in one mating of zero records, and (*d*) the sharp break within the 'Under 30' class, especially to be noted in mating 699, but also clear in each of the others.

Now these four matings were remarkable in other respects than the egg records of the progeny. They gave an extraordinarily high hatching record. This is shown in table 32.

Considering that these figures include all eggs set during the whole hatching season it is evident that the record is relatively very high. In a former paper (30) I have shown (loc. cit., table B, p. 131) that for the high laying Barred Rock matings the mean percentage of fertile eggs was 80.7 per cent., while 55.1 per cent of the fertile eggs were hatched. Even those

TABLE 32

Showing the hatching records of ♂ 578's F_2 matings

Mating	Eggs Set	Eggs Infertile	Eggs Fertile	Chicks Hatched
699	58	0	58	46
700	57	0	57	37
701	37	1	36	27
702	49	5	44	37
Totals.....	201	6	195	147

Per cent. of eggs fertile = 97.01.
Per cent. of fertile eggs hatched = 75.38.

results could only be considered very good taking all the facts into consideration. These back-cross matings of ♂ 578 far surpass those records.

One can only conclude that for some reason not apparent the matings 699 to 702 were physiologically extremely favorable. There seems to have been a what the breeders call a 'nick' here of unusual character. These matings were noticeable throughout the hatching season not only for the large number of the chicks produced, but also for their extra fine, vigorous character. The chick mortality from these matings was low

As has been pointed out at the beginning of this section of the paper, there undoubtedly exist differences in what might be called physiological compatibility between fowls of different genotypic constitutions. Some concrete data regarding this have been published in a previous paper (39). More will be presented later. While some gametic combinations (at least at their first synthesis) lead to physiologically weak and abnormal individuals, others produce individuals which in vigor, rate of growth, etc., surpass the normal. This phenomenon is perhaps more clearly and strikingly shown in pre-natal mortality (embryos dead in shell) than by any other character in fowls which can readily be measured. I hope shortly to publish a paper on this subject, and will only anticipate that paper here to the extent of saying that all the experience in this laboratory with cross-bred poultry agrees in showing that while there may be differences in the ease or success with which fertilization of the egg occurs in breed crosses, these are relatively unimportant as compared with the differential embryonic mortality. The proportion of embryos which start to develop, but lack the power to complete development is uniformly much greater for some hereditary combinations than for others, regardless of the particular individuals used as parents, and under uniform conditions of incubation and of housing and feeding the parent stock.

It is in this direction that I am inclined to look for the explanation of the discordant results of ♂ 578's matings with barred F_1 females. The records give one the impression that the potency or absolute fecundity value of the several gametic factors had, because of the super-normal physiological condition, been bodily raised considerably above the normal for the strains used in these experiments. One cannot escape the feeling that all these birds were making higher records than individuals of the same gametic constitution but of more ordinary physiological character in general would have done. The scale of fecundity values has apparently shifted in an upward direction; in other words something similar to what occurs when two inbred strains of maize are crossed happened here.

Along this line is the only explanation for the outcome of these four matings that I am able to suggest. It is quite possible that it may have no bearing, and that the results are due to some peculiarity of gamete formation which can be suggested

by some one. Personally, however, I am more inclined to keep to the solid ground of the observed physiological peculiarities of these matings rather than to 'juggle the genes.' Even in the hands of an adept in this direction, which the writer cannot claim to be, the latter procedure runs some risk of taking one a great way from any solid ground of fact whatever.

Regarding these four matings 699-702 the following facts are definitely known:

1. High fertility of eggs.

2. Smallest embryonic (pre-natal) mortality of any *particular* gametic combination yet experienced in the work of this laboratory.

3. Great vigor and vitality of chicks at hatching and during growth.

4. Very low chick and adult mortality.

5. A higher egg production in practically all adult daughters than would be expected from the gametic constitutions *per se* of the parent forms, the latter being definitely known from their pedigrees and from their behavior (§ 578), or that of their full sisters in other types of matings.

I cannot escape the conviction that in some way the first four of these facts are connected with the explanation of the fifth. There the matter must be left for the present.

This case points to the importance of the physiological study of individuals in genetic work involving crossing. Only the most superficial aspects of this subject have ever been touched. The 'increased vegetative vigor' of first crosses is clear in some instances, but very far from being so in others, and nobody has ever shown by a clean-cut physiological investigation why or how the phenomenon occurs. Every breeder of experience knows that this is but one of many interesting and fundamentally significant physiological matters in connection with hybridizing and cross-breeding which need investigation. The animal breeder knows further that there are real objective phenomena, and not mere idle superstitions of the fancier at the basis of those things which the latter calls 'nicking' and 'prepotency,' for example. No doubt these things depend on simple

genetic laws, but the point is that we do not now know scarcely anything definite (i.e., scientifically exact) about the phenomena, to say nothing of their underlying laws. The richness of the field which still remains quite unworked on the purely physiological side of genetics is, I think, only appreciated by the experienced breeder.

Summary and Discussion of Results

The facts and their interpretation

In this paper is presented a detailed analysis and interpretation of a rather extensive series of data regarding the inheritance of fecundity in the domestic fowl. The basic data are derived from trap-nest records extending over a period of years. They include records from (*a*) pure Barred Plymouth Rocks; (*b*) Cornish Indian Games; (*c*) the F_1 individuals obtained by reciprocally crossing these two breeds; and (*d*) the F_2 individuals obtained by mating the F_1's *inter se* and back upon the parent forms in all possible combinations. The fully-pedigreed material made use of in this present paper includes something over a thousand adult females, each of which was trap-nested for at least one year, and many for a longer period. This material covers four generations. The birds of the fifth generation have just completed their winter records at the time of writing. Besides this fully pedigreed material, the collection and study of which has occupied five years there was available as a foundation, without which the results discussed in this page could not have been reached, nine years of continuous trap-nest records for Barred Plymouth Rocks, involving thousands of birds, which had been subjected during this long period to mass selection for increased egg production.

Altogether it may fairly be said that the material on which this paper is based is (*a*) large in amount, (*b*) extensive in character, and (*c*) in quality as accurate as it is humanly possible to get records of the egg production of fowls (Pearl 31). On these accounts the facts presented are worthy of careful consideration, and have a permanent value quite apart from any interpretation which may be put upon them.

The essential facts brought out in this study of fecundity appear to me to be the following:

1. The record of fecundity of a hen, taken by and of itself alone, gives no definite, reliable indication from which the probable egg production of her daughters may be predicted. Furthermore mass selection on the basis of the fecundity records of females alone, even though long continued and stringent in character, failed completely to produce any steady change in type in the direction of selection.

2. Fecundity must, however, be inherited since (*a*) there are widely distinct and permanent (under ordinary breeding) differences in respect of degree of fecundity between different standard breeds of fowls commonly kept by poultrymen, and (*b*) a study of pedigree records of poultry at once discovers pedigree lines (in some measure inbred of course) in each of which a definite, particular degree of fecundity constantly reappears generation after generation, the 'line' thus 'breeding true' in this particular. With all birds (in which such a phenomenon as that noted under *b* occurs) kept under the same general environmental conditions such a result can only mean that the character is in some manner inherited.

The facts set forth in paragraphs 1 and 2 have been presented, and, I believe, fully substantiated by clean-cut and extensive evidence, in previous papers from this laboratory. In the present paper it is further shown that:

3. The basis for observed variations in fecundity is not anatomical. The number of visible oöcytes on the ovary bears no definite or constant relation to the actually realized egg production.

4. This can only mean that observed differences (variations) in actual egg productions depend up on differences in the complex physiological mechanism concerned with the maturation of oöcytes and ovulation.

5. A study of winter egg production (taken for practical purposes as that from the beginning of the laying year in the early fall to March 1) proves that this is the best available measure of innate capacity in respect to fecundity, primarily because it represents the laying cycle in which the widest difference

exists between birds of high fecundity and those of low fecundity.

6. It is found to be the case that birds fall into three well-defined classes in respect to winter egg production. These include (*a*) birds with high winter records, (*b*) birds with *low* winter records, and (*c*) birds which do not lay at all in the winter period (as defined above). The division point between *a* and *b* for the Barred Plymouth Rock stock used in these experiments falls at a production of about 30 eggs.

7. There is a definite segregation in the Mendelian sense of the female offspring in respect to these three fecundity divisions.

8. High fecundity may be inherited by daughters from their sire, independent of the dam. This is proved by the numerous cases presented in the body of this paper where the same proportion of daughters of high fecundity are produced by the same sire, whether he is mated with dams of low or of high fecundity.

9. High fecundity is not inherited by daughters from their dam. This is proved by a number of distinct and independent lines of evidence, of which the most important are: (*a*) continued selection of highly fecund dams does not alter in any way the mean egg production of the daughters (26, 27, 28, 30, 34, 35, 36, 37); (*b*) the proportion of highly fecund daughters is the same whether the dam is of high or of low fecundity, provided both are mated to the same male;[16] (*c*) the daughters of a highly fecund dam may show either high fecundity or low fecundity, depending upon their sire; (*d*) the proportion of daughters of *low* fecundity is the same whether the dam is of high or of low fecundity provided both are mated to the same male.

10. A low degree of fecundity may be inherited by the daughters from either sire or dam or both.

11. The results respecting fecundity and its inheritance stated in paragraphs 3 to 10 inclusive are equally true for

[16] This is true, of course, only for certain gametic types of low fecundity females, as will be clear to anyone who has studied the detailed evidence. This limitation, however, in nowise diminishes the force of this particular evidence in favor of the conclusion standing at the beginning of paragraph 9.

Barred Plymouth Rocks, Cornish Indian Games, and all cross-bred combinations of these breeds in F_1 and F_2.[17]

The above statements are of definite facts, supported by a mass of evidence. Their truth is objective and depends in no way upon any theory of inheritance whatsoever. With this clearly in mind we may undertake their interpretation.

It is believed that these general facts, and the detailed results on which they are based, are completely accounted for and find their correct interpretation in the simple Mendelian hypothesis respecting the inheritance of fecundity in the fowl, which was outlined at the beginning of this paper and has been checked against the detailed data from each mating. This hypothesis involves the following points, each of which is supported by direct and pertinent evidence derived either from physiological and statistical studies of fecundity, or from the detailed data respecting the mode of inheritance of this character.

It is assumed in this hypothesis that:

1. There are three distinct and separately inherited factors upon which fecundity in the female fowl depends.

2. The first of these factors (which may be called the anatomical) determines the presence of an ovary, the primary organ of the female sex. The letter F is used throughout to denote the presence of this factor.

3. There are two physiological factors. The first of these (denoted by L_1) is the basic physiological factor, which when present alone in a zygote with F brings about a low degree of fecundity (winter record under 30 eggs). This factor is under no limitations in gametogenesis but may be carried in any gamete, regardless of what other factors may be also present.

4. The second physiological factor (denoted by L_2) when present in a zygote together with F and L_1 leads to a *high* degree of fecundity (winter record over 30 eggs). When L_1 is absent, however, and L_2 is present the zygote exhibits the same general degree of fecundity (under 30) which it would if L_1 were present alone. These two independent factors L_1 and L_2

[17] And F_3. It has not been thought wise to delay publication of this paper any longer in order to include the data for F_3. It may be said however that they are in full accord with those which have been obtained from earlier cross-bird generations and the parent forms.

must be present together to cause high fecundity, either of them alone, whether present in one or two 'doses,' causing the same degree of low fecundity.

5. The second physiological factor L_2 behaves as a sex-limited (sex-correlated or sex-linked) character, in gametogenesis, according to the following rule: the factor L_2 is never borne in any gamete which also carries F. That is to say, all females which bear L_2 are heterozygous with reference to it. Any female may be either homozygous or heterozygous with respect to L_1. Any male may be either homozygous or heterozygous with reference to either L_1, L_2 or both.

How well this hypothesis agrees with the facts has been shown in detail in the preceding sections. By way of summary the following table shows the accord between observation and expectation for all matings of each general type taken together. For reasons set forth below, the lumped figures do not give an

TABLE 33

Showing the observed and expected distributions of winter egg production for all matings taken together

Mating	Winter Production of Daughters			
	Class	Over 30	Under 30	Zero
All B. P. R. × B. P. R.	Observed	365½	259½	31
	Expected	*381.45*	*257.25*	*17.30*
All C. I. G. × C. I. G.	Observed	2	23	15
	Expected	*0*	*25*	*15*
All F_1	Observed	36	79	8
	Expected	*26.5*	*88.75*	*9.75*
All F_2 and back-crosses[1]	Observed	57½	98½	23
	Expected	*68.60*	*95.00*	*15.40*

[1] With exception of the matings of C. I. G. ♂ 578 m Barred F_1 ♀ ♀. Cf. p. 246.

altogether fair estimate of the matter, but some sort of a summary is necessary.

Considering the nature of the material and the character dealt with it can only be concluded that the agreement between observation and hypothesis is as close as could reasonably be expected. The chief point in regard to which there is a discrepancy is in the tendency, particularly noticeable in the B.P.R. × B.P.R. and the F_2 matings, for the observations to be in defect

in the 'Over 30' class and in excess in the 'Zero' class. The explanation of this is undoubtedly, as has been pointed out in the body of the paper, to be found in disturbing physiological factors. The high producing hen, somewhat like the race horse, is a rather finely strung, delicate mechanism, which can be easily upset, and prevented from giving full normal expression to its inherited capacity in respect to fecundity.

In order to forestall any possible change of manipulation of the data to support a particular hypothesis all of the figures (with the exception of 7 birds discussed on p. 360 and the F_2 mating of ♂ 578) have been entered throughout exactly as they stood on the original books of record. That is to say, some birds known to be physiologically abnormal or pathological have not been rejected, but have been entered in the tables and then discussed in the accompanying text. Whether this is accounted a justifiable procedure or not will depend upon one's point of view in some degree. The investigator is usually expected to reject abnormal material. But in view of the rather hysterical attacks upon geneticists and their method of work now becoming so fashionable in this country, if for no other reason, it seems best to follow the plan of publishing all the data. The opponents to the views which underlie the Mendelian interpretation here advanced are quite welcome to make as much capital as they are able to out of the discrepancies between observation and theory in the several tables. It seems only fair, however, to ask that a judgment of the adequacy of the hypothesis be not formed from this summary table 33, but instead from the detailed data in the body of the paper.

Possible criticisms

In consideration of the fact that this paper constitutes one of the first attempts to apply a Mendelian interpretation to the facts regarding the inheritance of an economically productive character of an animal, and in view of the possible application of the results or the methods of this paper to other productive characters of other organisms it is important to examine carefully and critically the nature of the evidence and the objections which may be brought against the conclusions. In the first place it is important to note once more that the data and their interpreta-

tion are kept separate throughout, and that the value of the former is not lessened if the latter is later found to be completely invalid, or in need of modification. It is carcely necessary to say that the Mendelian hypothesis here presented is the only simple one which the writer has been able to discover, after over two years of study directed (whenever the time was available) towards this particular end, which is capable of accounting satisfactorily for all the facts. Very many other Mendelian schemes for the inheritance of fecundity have been tested against the facts in the course of the work and discarded, one by one, because inadequate. Of course, it still remains quite possible, though perhaps not very probable, that there may be an even simpler hypothesis which will equally well or better account for the facts. If so, by all means let us have it. But in the meantime, it may be fairly be said, that the hypothesis here presented brings together under a few, symbolically simple, general statements a wide range of very diverse and complex facts of inheritance.

The strongest general evidence that the Mendelian hypothesis here presented is at least a close approximation to the truth in respect to the inheritance of a fecundity in the fowl is found in the fact that it accounts equally well for so wide a range of diverse phenomena. In the two 'pure' parent races, one of generally high and the other of generally low fecundity; the two reciprocal crosses; and the twelve different kinds of matings in F_2, we have a series of really independent measures of the validity of the hypothesis. It accords with the facts in all but one (the matings of C.I.G. ♂ 578 with Barred F_1 ♀ ♀) of all of the different types of matings tested. The one exception probably has a physiological explanation (pp 373-377). In view of these facts the cumulative probability that the hypothesis applied represents at least a reasonable approximation to the true interpretation of the results becomes very great.

A possible criticism of the whole method of this investigation might be found in reference to the measure of fecundity which has been used throughout, namely, the winter egg production. Regarding this matter it should be said that the very reason why winter egg production was adopted as the unit of measure in all of the fecundity work of this laboratory was because a thor-

ough biometrical and physiological study of egg production in fowls howed beyond question that winter production was the best practicable index or measure of a fowl's innate or constitutional capacity in respect of fecundity. The reasons for this conclusion have been set forth in this and former papers from the laboratory and need not be repeated *in extenso* here. The most significant of them is that the differences in observed production between individuals of different innate fecundity capacities are relatively greater in respect of winter productions than of any other time unit that can practically be employed in the measuring of this character. To suppose, however, that the results set forth in this paper depend for their existence upon the use of this particular time period of production as a measure of fecundity has no warrant in fact. Precisely the same results (in principle) would be obtained if yearly production records were used in the analysis. During the whole of this work complete yearly records have been kept and have been studied. They show in every essential particular the same kind of results as those of this paper. There are objections to the use of the year as a unit of measure, however, which may not be obvious to one inexperienced in these matters. In the first place, it is very much more difficult to keep large flocks of hens in normal, and healthy physiological condition over a whole year period than over a shorter period. Again the risk of an accident (say the use of bad feed or something of the kind) occurring and upsetting the birds physiologically, and coincidently rendering their fecundity records abnormal and in greater or less degree useless, is increased just in proportion as the time unit is increased. Further the year period includes as a too dominant feature, the spring egg production. The production during the months of March, April and May is practically worthless (and has long been so recognized by experienced poultrymen) as an index or measure of the true, innate or constitutional fecundity capacity of the individual. During these months (in northern latitudes) all hens which are not diseased, malformed, infantile or senile, lay anywhere from 'well' to 'very well.' There is relatively little difference between the most and the least fecund at this season. This period is therefore worthless as a measure of fecundity, and its inclusion in any longer period makes that by so much the less valuable as a measure.

In view of all these considerations it seems certain that the results obtained are not open to criticism on the ground of the time unit used as a measure of fecundity.

Another matter which needs careful consideration is as to the possibility of unconscious bias having influenced the results themselves. In other words, to what extent does the personal equation factor enter into this fecundity work? It can be fairly said, I think, that there is less opportunity for unconscious bias to affect the results here than in genetic work on most other characters. The reason is because of the impersonal and objective character of the original records in the case of fecundity. The original trap-nest records on which this whole study is based were made by Mr. F. Walter Anderson. He had neither knowledge of, nor interest in, the use of which any particular record or set of records were to be put. He was solely concerned to make as accurate record as possible of the laying of each individual hen. The system of record taking used is such that it was impossible for him to have any notion of what the total production of any given bird up to a particular date had been. The chance for bias or personal equation influencing results is excluded when, as in the present case, one person makes the basic records, and has nothing whatever to do with their analysis, while another person analyzes the data but has nothing directly to do with their collection.

Another safeguard on the results in this same direction, and also in another, is found in the fact that birds belonging to the same family (full sisters) were not given identifying numbers which would make it possible to be certain or even to surmise that they were sisters, without consultation of the pedigree records. The numbering of the birds for identification each year was purely at random and without any regard whatsoever to relationship. Furthermore members of the same family were distributed at random through the different pens and houses. No attempt is ever made, from the day the chicks hatch, to keep the birds from one family together. Indeed it is important that they be scattered at random through the flock in order to insure uniformity of *average* environmental conditions.

The writer has no desire to generalize more widely from the facts set forth in this paper than the actual material experimen-

tally studied warrants. It must be recognized as possible, if not indeed probable, that other races or breeds of poultry than those used in the present experiments may show a somewhat different scheme of inheritance of fecundity. The directions in which deviations from the plan here found to obtain may, at least *a priori*, most probably be expected are two. These are: (*a*) differences in different breeds in respect to the absolute fecundity value or worth of the factors which determine the expression of this character, and (*b*) gametic schemes which differ from those here found either in the direction of more or fewer distinct factors being concerned in the determination of fecundity, or in following a totally different type of germinal reactions.

Regarding the first point it will be recalled that in several places in the body of the paper it has been suggested that the absolute fecundity value (i.e., the degree of actual fecundity determined by the presence of the gametic factor) may differ for the factor L_1 in the case of the Barred Rock as compared with the Cornish Indian Game breed. It is hoped later to take up a detailed study of this point, on the basis of the material here presented, and additional data now in process of collection. Wherever there is a difference in the absolute fecundity value of the L_1 factor, it means that the division point for the classification of winter productions should be taken at a point to correspond with the physiological facts. In this first study the division at 30 eggs has been found to accord sufficiently well for practical purposes with the actual facts. Similarly the absolute fecundity value of the excess production factor L_2 may be different in different breeds. In applying the results of this paper to the production statistics of other breeds of poultry the possibility of differences of the kind here suggested must always be kept in mind.

The second point (the possibility of gametic schemes for fecundity differing qualitatively from that found in the present study) is one on which it is idle to speculate in advance of definite investigations. I wish only to emphasize that nothing is further from my desire or intention than to assert before such investigations have been made that the results of the present study apply unmodified to all races of domestic poultry.

It cannot justly be urged against the conclusions of this study that the Mendelian hypothesis advanced to account for the results is so complicated, and involves the assumption of so many factors or such complex interactions and limitations of factors, a to lose all significance. As a matter of fact the whole Mendelian interpretation here set forth is an extremely simple one, involving essentially but two factors. This surely does not indicate excessive complication. To speak in mathematical terms, by way of illustration merely, it may fairly be said, that the formula here used to 'fit' the data, has essentially the character of a true graduation formula, rather than that of an interpolation formula. The number of constants (here factors) in the formula is certainly much less than the number of ordinates to be graduated.

There is no assumption made in the present Mendelian interpretation which has not been fully demonstrated by experimental work to hold in other cases. That the expression of a character may be caused by the coincident presence of two (or more) separate factors, either of which alone is unable to bring it about, has been shown for both plants[18] and animals by a whole series of studies in this field of biology during the last decade. To find examples one has only to turn to the standard hand-books summarizing Mendelian work, as for example those of Bateson and Baur. Again sex-linkage or correlation of characters in inheritance has been conclusively demonstrated for several characters in fowls by the careful and thorough experiments of a number of independent investigators. Finally it is to be noted that Bateson and Punnett (4) have recently shown that the inheritance of the peculiar pigmentation characterictic of the silky fowl follows a scheme which in its essentials is very similar to that here worked out for fecundity.

The selection problem

The results of the present investigation have an interesting and significant bearing on the earlier selection experiments on fecundity at this Station. It is now quite plain that continued selection of highly fecund females alone could not even be ex-

[18] Particularly important here are the brilliant researches of Nilsson-Ehle (24, 25) on cereals, and of Baur (2) on *Antirrhinum*.

pected to produce a definite and steady increase in average flock production. The gametic constitution of the male (in respect especially to the L_2 factor) plays so important a part in determining the fecundity of the daughters that any scheme of selection which left this out of account was really not 'systematic' at all but rather almost altogether haphazard. It has been repeatedly shown in the body of the paper that the same proportion of daughters of high fecundity may be obtained from certain mothers of low fecundity as can from those of high fecundity, provided both sets of mothers are mated to males of the same gametic constitution. What gain is to be expected to accrue from selecting high laying mothers under such circumstances, at least so far as concerns the daughters?

'Selection' to the breeder means really a system of breeding 'Like produces like,' and 'breed the best to get the best;' these epitomize the selection doctrine of breeding. It is the simplest system conceivable. But its success as a system depends upon the existence of an equal simplicity of the phenomena of inheritance. If the mating of two animals somatically a little larger than the average always got offspring somatically a little larger than the average, breeding would certainly offer the royal road to riches. But if, as a matter of fact, as in the present case, a character is not inherited in accordance with this beautiful and childishly simple scheme, but instead is inherited in accordance with an absolutely different plan, which is of such a nature that the application of the simple selection system of breeding could not possibly have any direct effect, it would seem idle to continue to insist that the prolonged application of that system is bound to result in improvement.

It seems to me that it must be recognized frankly that whether or not continued selection of somatic variations can be expected to produce an effect on the race depends entirely on the mode of inheritance of the character selected. In other words, any systematic plan for the improvement of a race by breeding must be based and operated on a knowledge of the gametic condition and behavior of the character in which improvement is sought rather than the somatic. Continued mass selection of somatic variations as a system of breeding, in contrast to an intelligent plan based on a knowledge of the gametic basis of a character and how it is inherited, seems to me to be very much

in the same case as a man who, finding himself imprisoned in a dungeon with a securely locked and very heavy and strong door with the key on the inside, proceeded to attempt to get out by beating and kicking against the door in blind fury, rather than take the trouble to find the location of the key and unlock the door. There is just a possibility that he could finally get out in a very few instances by the first method, but even in those cases he would be regarded by sensible men as rather a fool for his pains.

Of course what has been said is not meant to imply that selection on the basis of somatic conditions may not have a part in a well considered system of breeding for a particular end. In many cases it certainly will have. Thus in the case of fecundity in the fowls, selection of mothers on the basis of fecundity records is essential in getting male birds homozygous with respect to L_1 and L_2. But the point which seems particularly clear in the light of the present results is that blind mass selection, on the basis of somatic characters only is essentially a haphazard system of breeding which may or may not be successful in changing the type in a particular case. There is nothing in the method *per se* which insures such success, though that there is inherent potency in the method *per se* is precisely the burden of a very great proportion of the teaching of breeding (in whatever form that teaching is done) at the present time.

It seems to me that it has never been demonstrated, up to the present time, that continued selection can do anything more than:

1. Isolate pure biotypes from a mixed population, which contains individuals of different hereditary constitution in respect to the character or characters considered.

2. Bring about, as a part of a logical system of breeding for a particular end, certain combinations of hereditary factors which would never (or very rarely) have occurred in the absence of such systematic selection; which combinations give rise to somatic types which may be quite different from the original types. In this way a real evolutionary change (i.e., the formation of a race of qualitatively different hereditary constitution from anything existing before) may be brought about. This can unquestionably be done for fecundity in the domestic fowl.

But here 'selection' is simply one part of a system of breeding, which to be successful must be based on a definite knowledge of gametic as well as somatic conditions. It is very, very far removed from a blind 'breeding of the best to the best to get the best.' The latter plan alone may, as in the case of fecundity, fail absolutely to bring about any progressive change whatever.

It has never yet been demonstrated, so far as I know, that the absolute somatic value of a particular hereditary factor or determinant (i.e., its power to cause a quantitatively definite degree of somatic development of a character) can be changed by selection on a somatic basis, however long continued. To determine, by critical experiments which shall exclude beyond doubt or question such effects of selection as those noted under 1 and 2 above, whether the absolute somatic value of factors may be changed by selection, or in any other way, is one of the fundamental problems of genetics.

Prepotency

One of the least understood phenomena in genetics is that which the practical breeder calls 'prepotency.' When the scientific student of genetics deals with the matter at all he is rather apt either to throw it over entirely as a 'breeder's superstition,' or to take it as something 'given' to help him out of a difficulty in the interpretation of results which fail to conform to expectation. Some time a more searching investigation of this phenomenon must be made than is implied in either of these lines of procedure.

In a former paper (27, p. 324), it was suggested that the evidence indicated, for certain productive characters at least, that hereditary high performance tended to behave as a Mendelian dominant to hereditary low performance. The following statement was then made:

"If this suggestion is true it gives at once, I think, a possible clue to the explanation of a part at least of the known facts regarding what is called prepotency in the practical breeding of domestic animals for performance. It is customary in practice to regard an animal as prepotent in breeding for performance when the progeny of that individual uniformly tend to resemble it closely in respect to the character bred for, regardless of the other parent in each mating. Let it now only be considered

that the great sire, say, of speed or of milk production belongs to a line having a high genotype with regard to those characters; then it is to be expected, on the hypothesis under consideration, that his progeny will tend on the average to be like himself in performance regardless of what he is mated with, because any female to which he is mated will be either of a high genotype like himself or of a lower one. But if genotypic high performance is dominant over genotypic lower performance, than all the offspring in the first generation must approximate to the high condition exemplified in the sire. But this is the very essence of what is called prepotency in actual breeding practice."

It seems to me that certain of the facts set forth in this paper give strong support to this view. A class 1 B.P.R. ♂ ($= fL_1L_2$. fL_1L_2) will get all high producing daughters (barring physiological defects of development) regardless of the females to which he is mated. He will show all the objective phenomena of 'prepotency.' B.P.R. ♂ 550 is an example of this. A class 7 B.P.R. male would, in breeders' parlance, be regarded as less prepotent then a class 1 male, but, even so, more prepotent than the general run of the flock.

The essential point here should not be misunderstood. It is not, of course, contended that simple Mendelian 'dominance' in general, and prepotency are the same thing. More than that is demanded. It is only suggested that a homozygous dominant individual, when high performance is dominant over low, has all the objective characteristics of a prepotent individual in the breeder's sense.

That this suggestion explains all the facts regarding prepotence is by no means asserted. It seems to me, however, that it does furnish the explanation for a part of the phenomena at least, and by so much helps towards a final solution, since it brings us nearer to the kernel of the problem.

The practical bearing of these results

To the practical poultryman the data and conclusions of this paper would appear to have some significance. They make it possible to outline a scheme of breeding for increased egg production which shall be intelligently directed towards the attainment of that end. This, however, is not the place to discuss such a scheme. That will be undertaken later in another place.

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